Phylogenetic Systematics and Biogeography of the Carphodactylini (Reptilia: Gekkonidae)

by

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BONNER ZOOLOGISCHE MONOGRAPHIEN

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CONTENTS

ABSTRACT

The tribe Carphodactylini is composed of 49 species of geckos of the subfamily Diplodactylinae that are endemic to the regions of Australia, New Caledonia and New Zealand. The systematics of the group is approached through the methodology of phylogenetic systematics and a hypothesis of genealogical relationship is presented. The padless Australian genera *Nephrurus* (including *Underwoodisaurus*), *Phyllurus*, and *Carphodactylus* are the sister group of the New Caledonian and New Zealand carphodactylines. The New Zealand genus *Hoplodactylus* is paraphyletic. The New Caledonian taxa (*Bavayia, Eurydactylodes*, and *Rhacodactylus*) form a monophyletic unit if the northern Australian genus *Pseudothecadactylus* is regarded as a subgenus of *Rhacodactylus*. Systematic accounts and summaries of all biological literature relating to each species are presented.

The tectonic history of the southwest Pacific region is in harmony with the hypothesis of carphodactyline relationships. The primary division of the tribe into Australian and Tasmantis lineages was probably brought about by the opening of the Tasman Sea about 80 mybp. By the Oligocene marine ingressions isolated New Caledonia from northern New Zealand, thus splitting *Hoplodactylus*. Carphodactyline geckos highlight the antiquity, endemism and biogeographic significance of the herpetofauna of the southwest Pacific, and New Caledonia in particular.

INTRODUCTION

Although a great deal of systematic work has dealt with the place of gekkonids among squamates and with higher order relationships among geckos, little has been produced with respect to inter- and intrageneric relationships within the tribe Carphodactylini. The carphodactylines as currently construed include the Australian genera *Nephrurus, Phyllurus, Carphodactylus* and *Pseudothecadactylus*, the New Zealand genera *Naultinus* and *Hoplodactylus*, and the genera *Bavayia, Eurydactylodes* and *Rhacodactylus* from New Caledonia and the Loyalty Islands. In addition, *Underwoodisaurus* (Australia) and *Heteropholis* (New Zealand) are also occasionally recognized as distinct taxa at a generic level. The present work is an attempt to summarize that which is known about carphodactyline biology and to erect a hypothesis of relationship upon which subsequent evolutionary morphological studies may be based. (In the pages that follow, in order to avoid confusion, nomenclatural changes implemented as a result of this study are used consistently from the start — e.g., *Nephrurus milii* instead of *Phyllurus milii* or *Underwoodisaurus milii*).

The earliest reviewers of lizard taxonomy were perplexed by the taxonomic affinities of the first described carphodactyline, *Phyllurus platurus* (White 1790). Schneider (1797), Daudin (1802), La Cépède (1804), and Merrem (1820) all placed the species in an agamid genus, either *Agama* or *Stellio*. Gray (1825) was uncertain as to its affinities, but suggested links with either the agamids or gekkonids. Bory de Saint-Vincent (1825)

described a second species, *P. milii* (= *Nephrurus milii*), recognized its similarity to *P. platurus*, and assigned both to the Gekkonidae.

Fitzinger (1843) distributed the four species known to him into three genera in two families of the Ordo Ascalabotae. The family Stenodactyli, essentially containing all geckos without dilated scansorial subdigital pads, included *Gymnodactylus miliusii* and *Gonyodactylus platurus*, the latter genus being distinguished by a prominent kink in the digits. The remaining taxa, *Hoplodactylus duvaucelii* and *Hoplodactylus (Rhacodactylus) leachianus*, were included among the Platydactyli, a mixture of all of the padded geckos without divided or lobed scansors. This classification system, like most of those which followed for over one hundred years, made no attempt at phylogenetic analysis but rather pigeon-holed species primarily on the basis of external digital characters.

Gray (1845) keyed *Phyllurus* and *Naultinus* to the same first subdivision of geckos while separating *Platydactylus* (including *Rhacodactylus* and *Hoplodactylus duvaucelii*). Girard (1858) relied on artificial divisions to yield information about natural groups ("the genus *Naultinus* is a Stenodactylian: hence widely distinct from *Hoplodactylus*, which . . . is a Platydactylian").

Boulenger (1885a) accorded no special recognition to the group now regarded as the Carphodactylini. His division in the "Catalogue of Lizards" was based on the order in which genera fell out in the family keys. Nevertheless, the structure of the keys, while largely artificial, may imply some phylogenetic information (Russell 1976). Boulenger's primary divisions were based upon pedal structure and the carphodactylines known at the time were distributed among five different major groups of geckos. Notably, division VII lists the genera *Naultinus, Hoplodactylus* and *Rhacodactylus* in sequence. These are immediately preceded by *Lepidodactylus* which at the time included the species later transferred to *Bavayia*. Although clustered together because of digital similarities, the particular order of these genera may reflect Boulenger's belief in some sort of close relationship among these taxa, a belief that would have been supported by biogeographical data.

Gadow (1901), Werner (1912), Camp (1923) and Smith (1933a), while shuffling the taxonomic rank of the eublepharine geckos and the Madagascan *Uroplatus*, made no distinction as to the taxonomic subdivision of the majority of the Gekkonidae. Roux (1913), however, did suggest that the New Caledonian genera *Rhacodactylus, Eurydactylus (= Eurydactylodes)* and *Bavayia* might share affinities with *Hoplodactylus*, based upon their possession of an offset terminal pad on digit one.

Underwood (1954) provided the first attempt at a reexamination of the higher systematics of geckos. His division of the Gekkonidae into the subfamilies Diplodactylinae and Gekkoninae was based primarily on the structure of the pupil in life; straight-edged in the former and a series of pinholes ("*Gekko*-type") in the latter. This distinction, while later challenged (Kluge 1964, 1967a; Cogger 1964), was effective in delineating the patterns of subfamilial affinities that have since been vindicated by the work of Kluge (1967a, 1967b, 1982, 1983a, 1987) and others. Using the pupil-shape criterion Underwood successfully removed the ambiguity then present as to the distinc-

tion between species of *Diplodactylus* and *Phyllodactylus*. It also clarified the position of *Phyllurus* as distinct from other Old World *Gymnodactylus* (= *Cyrtodactylus* sensu Underwood). Underwood (1954) included within *Phyllurus*, in addition to *P. cornutus, P. milii* and *P. platurus*, the New Guinean *P. vankampeni*, which has since been identified as a gekkonine (Kluge 1967a).

T a b l e 1. Components of the Diplodactylinae (Underwood 1954) with corresponding tribal (Kluge 1967b for Diplodactylinae; Kluge 1983a for Gekkoninae) and generic group (Russel 1972) placements. AUS = Australia, NZ = New Zealand, NC = New Caledonia, SAF = Southern Africa, NAF = North Africa, ASI = Asia, WI = West Indes, SAM = South America. R = *Rhoptropus*-type pupil (sensu Underwood 1954).

Genus	Region	Tribe (Kluge 1967b, 1983a)	Generic group (Russel 1972)
Carphodactylus	AUS	Carphodactylini	
Nephrurus	AUS	Carphodactylini	
*Phyllurus**	AUS	Carphodactylini	
Diplodactylus	AUS	Diplodactylini	
Lucasius	AUS	Diplodactylini	
Oedura	AUS	Diplodactylini	
Rhynchoedura	AUS	Diplodactylini	
Hoplodactylus	NZ	Carphodactylini	
Naultinus	NZ	Carphodactylini	
Bavayia	NC	Carphodactylini	
Rhacodactylus	NC	Carphodactylini	
Chondrodactylus (R)	SAF	Ptyodactylini	*Pachydactylus*[1]
Colopus (R)	SAF	Ptyodactylini	*Pachydactylus*
Palmatogecko (R)	SAF	Ptyodactylini	*Pachydactylus*
Rhoptropus (R)	SAF	Ptyodactylini	*Pachydactylus*
Phelsuma (R)	SAF	Ptyodactylini	*Lygodactylus*[2]
*Rhotropella** (R)*	SAF	Ptyodactylini	*Lygodactylus*
Ptenopus (R)	SAF	Ptyodactylini	not placed
Saurodactylus	NAF	Ptyodactylini	not placed
Teratoscincus	ASI	Ptyodactylini	*Stenodactylus*[3]
Aristelliger	WI	Gekkonini	*Aristelliger*[4]
Gymnodactylus	SAM	Gekkonini	not placed

*   Includes *Cyrtodactylus vankampeni*
** Synonomized with *Phelsuma* by Russel (1977a)
[1] Also includes *Geckonia, Tarentola,* and *Kaokogecko* (not known to Underwood). Haacke (1976), Russel (1977a) and Kluge (1983a) found evidence for the monophyly of this generic group. Joger (1985) provided immunological support for the group as well, although he indicated that *Pachydactylus* itself is polyphyletic.
[2] Also includes *Ailuronyx, Microscalabotes, Millotisaurus*. Kluge (1983a) placed all members of this group, except *Phelsuma* in the Gekkonini.
[3] Includes only *Stenodactylus* and *Teratoscincus*.
[4] Placed in own species group.

In all, Underwood's (1954) Diplodactylinae included 22 genera (see Table 1), incorporating all but two of the genera now accepted as well as some members of a (probably monophyletic) group of South African gekkonines, *Saurodactylus*, the South American *Gymnodactylus* and two particularly odd gekkonines, *Teratoscincus* and *Aristelliger*. The last has been noted for its many convergent characters with diplodactylines (Russell 1979a; A. E. Greer pers. comm.) and its distinctive autapomorphies (Kluge 1982). A number of the remaining taxa possessed what Underwood referred to as the "*Rhoptropus*-type" pupil (Table 1). The removal of these taxa, now recognized as African gekkonines, would have left Underwood's Diplodactylinae slightly less polyphyletic.

Within the Diplodactylinae Underwood (1954) noted the similarities in the pollex among *Aristelliger, Bavayia* and *Rhacodactylus*. His views on the affinities of this group were strengthened by his contention that the three shared primitive features of the digits and eyes and that all "occupy peripheral positions in the total world range of geckos". This last statement is difficult to interpret given that geckos are pan-tropical and occur with great species diversity both in the West Indies and the Southwest Pacific.

Underwood (1954) ascribed two genera now recognized as carphodactylines to the Gekkoninae (*Pseudothecadactylus = Rhacodactylus* (part) and *Eurydactylus = Eurydactylodes*). While no particular mention is made of the former genus, the latter was discussed at some length. While placing this form in the Gekkoninae, Underwood indicated that it, along with *Oedura* and *Rhynchoedura*, required examination of living material as pseudo-"*Gekko*-type" pupil lobulation was suspected. Subsequently Underwood (1955, 1957) indicated that *Eurydactylus* was indeed a diplodactyline and that *Rhynchoedura* should be treated as a gekkonine. His statement "the six Australian, three New Caledonian, and two New Zealand diplodactyline genera form a well-defined tribe within the subfamily on osteological characters" (criteria unstated) essentially recognized a monophyletic Diplodactylinae (sensu Kluge 1967a, 1967b) with the exception of *Pseudothecadactylus* and *Rhynchoedura* and the retention of *Phyllurus (= Cyrtodactylus) vankampeni*.

Stephenson (1960), endorsed no particular theory of relationships, but criticized Underwood's single character methods and suggested that the use of another randomly chosen character might yield a different subdivision of the Australian geckos.

Werner (1961a, 1961b) accepted Underwood's scheme but drew rather different conclusions about evolution within the family. He stated that the New Zealand Diplodactylinae were the most primitive of the living geckos and derived the remaining three subfamilies from the diplodactylines. There are many inconsistencies within this scheme and the hypothesis of relationships it implies is supported by few synapomorphies. Werner based his hypothesis on the assumptions that the vertical pupil (present in *Naultinus*) is primitive, that the New Zealand diplodactylines have "a most primitive skeleton" (based on the claims of Stephenson & Stephenson 1956), and that narrow, padded toes are primitive for the family. Werner (1961b) further suggested that ovoviviparity might be primitive for geckos, having been lost in all non-New Zealand forms. These assumptions also require the independent evolution of eyelids in the

Eublepharinae and imply that eublepharines are secondarily padless (see discussion below). Further, procoely must evolve at least three times from an amphicoelous diplodactyline ancestor. This last character state transformation was apparently based on acceptance of Underwood's (1955) reversal of his previous, supported (see character analysis of axial skeleton) view (Underwood 1954) that procoely was primitive for the Gekkonidae. Werner's views were never published in their full form consequently not gaining wide acceptance. Werner's more recent work reflects a general acceptance of the hypotheses of relationship developed by Kluge (1967a).

Kluge (1965a, 1967a, 1967b), based on a wide variety of both osteological and soft characters, provided stability to the subfamilial divisions of the Gekkonidae and removed the African and New World components of Underwood's (1954) Diplodactylinae. He also provided the first explicit hypotheses of carphodactyline generic relationships. Based on the distribution of preanal pores and features of the nasal process of the premaxilla, Kluge (1965a, 1967b) divided the diplodactylines into two tribes, the Carphodactylini and the Diplodactylini.

Kluge (1967b) diagnosed the Carphodactylini on the presence of numerous rows of preanal pores arranged in a large, irregularly- shaped patch (Fig. 1), although *Bavayia sauvagii*, as well as the Australian genera *Nephrurus* and *Phyllurus*, show secondary modifications of this condition. Carphodactylines also possess a short, wide nasal process of the maxilla, but this character is plesiomorphic for the Diplodactylinae. Further, the presence of paired premaxillae throughout life is characteristic of the carphodac-
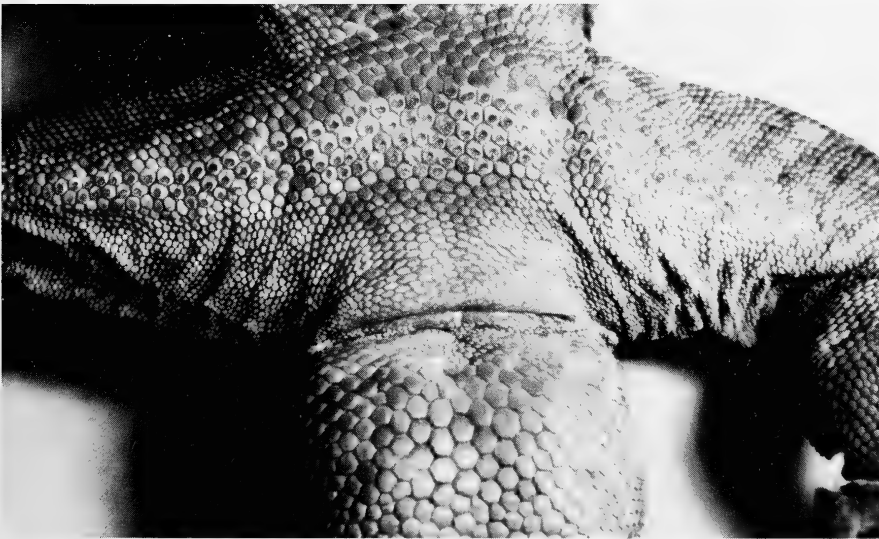

Fig.1: Ventral view of cloacal region of adult male *Hoplodactylus duvaucelii* showing the large patch of preanal organs, a synapomorphy of the Carphodactylini. (Photo courtesy of B.W. Thomas)

tyline genera (a reduced split, or partial fusion is seen in the New Zealand genera, *Rhacodactylus* and *Bavayia*).

The Diplodactylini, as well, were diagnosed by a series of synapomorphies by Kluge (1967b). The shared presence of the plesiomorphic condition for each of the characters used to diagnose the Diplodactylini was then used by Kluge as further evidence of carphodactyline relationships. Recent work by Kluge (1983a, 1987) employing the method of phylogenetic systematics has used only synapomorphies as evidence of shared ancestry.

Kluge (1965a, 1967b) believed that the tribe Carphodactylini possessed more primitive features than the Diplodactylini. Within carphodactylines he considered *Carphodactylus, Nephrurus* and *Phyllurus* to be most similar to the ancestral stock of the subfamily, with the latter two genera more closely related to each other than either is to *Carphodactylus*. Kluge also considered all three of the New Caledonian genera to be closely related, although he was uncertain of the relationship of *Bavayia* to the other genera. *Pseudothecadactylus* was considered to be more closely related to the New Caledonian radiation than to the main Australian radiation despite certain osteological similarities shared with the latter. Kluge accepted viviparity as evidence for the close phylogenetic relationship of the three New Zealand genera he recognized, and within this group considered *Hoplodactylus* and *Heteropholis* to be more closely related to each other than either was to *Naultinus*. The reason for this view, given the fact that *Naultinus* and *Heteropholis* cannot be diagnosed from one another, is unclear but probably results from Kluge's acceptance of the authority of McCann's (1955) "Lizards of New Zealand". This scheme of relationships is shown in Fig. 2.

It is unclear from Kluge's early work whether he accepted a monophyletic Carphodactylini. While he did provide a synapomorphy for the group he stressed the primitive aspects of the tribe and did not address the issue of padlessness in the Australian radiation. If it is accepted that this group is primitively padless (Russell 1972, 1979a) then pads must have evolved at least twice within the Diplodactylinae (and no padless Diplodactylini survived), or the Carphodactylini is paraphyletic, having given rise to the Diplodactylini.

Russell (1972), accepting the phylogeny of Kluge (1967a, 1967b), found that digital characters supported the unit *Carphodactylus* + *Nephrurus* + *Phyllurus* + *Underwoodisaurus* as a "compact group" and agreed with Kluge (1967b) that *Carphodactylus* was probably the most primitive extant member of the tribe (presumably because of the overall similarity to the eublepharine *Aeluroscalobotes*). Russell found no morphological intermediates between the primitively padless Australian genera and the padded forms of New Zealand and New Caledonia. He described a morphological series of increasing complexity in digital structure from *Heteropholis* through *Naultinus* to *Hoplodactylus*. Russell further considered the digital structure of the New Caledonian forms to be more advanced than that of their New Zealand relatives, and suggested that *Rhacodactylus* and *Eurydactylodes* were sister-taxa. *Pseudothecadactylus* was considered to be the most advanced genus in terms of pedal morphology and to share some similarities with *Rhacodactylus*.
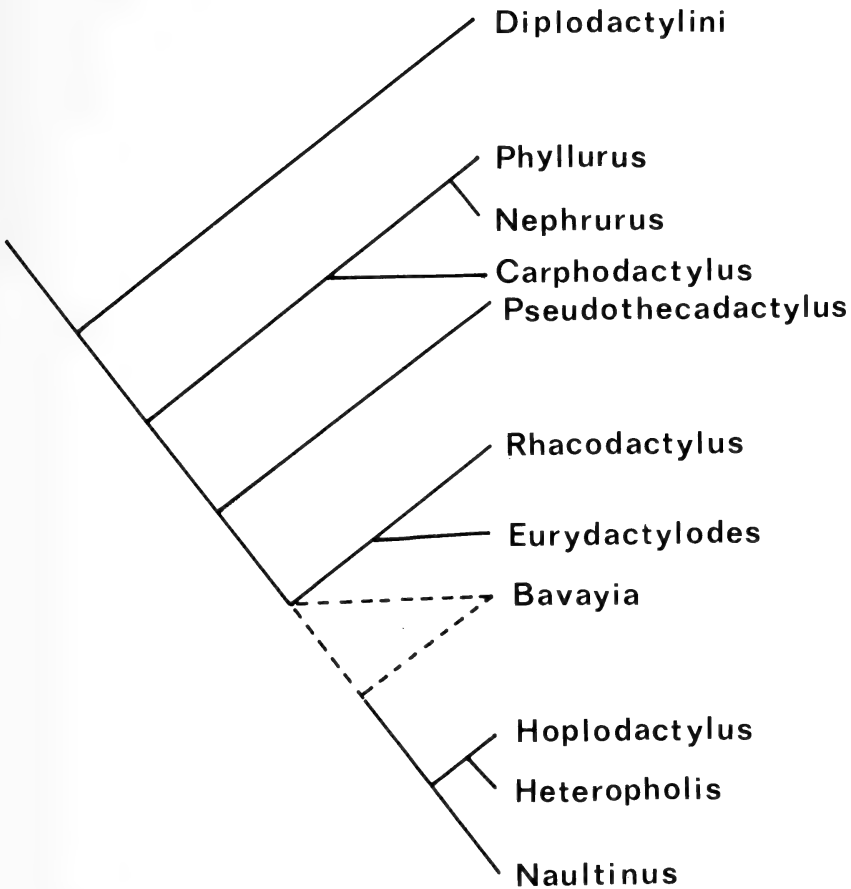
Fig.2: Tree diagram of hypothesized diplodactyline relations redrawn as a cladogram after Kluge (1965a, plate VI, Fig. 11).

Russell (1979a) later addressed the question of carphodactyline monophyly. He stated "the most parsimonious argument is that pads were acquired only once within this subfamily (the Diplodactylinae) . . . The basal stock of the Carphodactylini . . . was padless but it would appear that the Diplodactylini arose from an ancestor which possessed terminal subdigital pads". The acquisition of terminal pads is thus postulated as occurring before the separation of the Diplodactylini and the pad-bearing Carphodactylini. While this implies support for a polyphyletic Carphodactylini, Russell (pers. comm.) accepts the possibility that pads might have evolved twice within the Diplodactylinae — with a primarily distal enlargement in the Diplodactylini and a primarily basal enlargement in the padded carphodactylines. The existence of a well defined and supported Diplodactylinae and Gekkoninae + Sphaerodactylinae (Kluge

1987) necessitates parallel development of pads within geckos, even if the Carphodactylini is polyphyletic. Thus, convergent evolution of scansorial pads should not be ruled out within the Diplodactylinae on the grounds of parsimony.

Moffat (1973a) rejected Kluge's conclusions regarding subfamilial evolution but did not herself address the question of generic relationships within the subfamilies. Bull and Whitaker (1975), apparently without supporting data, suggested that the New Zealand genera of carphodactylines were directly derived from one or more New Caledonian genera. Hecht (1976) and Hecht & Edwards (1977) reevaluated the phylogenetic hypotheses of Underwood (1954), Kluge (1967a) and Moffat (1973a) but added little to the knowledge of intergeneric relationships.

Kluge (1987) revised his interpretations of diplodactyline phylogeny and biogeography. He provided explicit synapomorphies for the Diplodactylinae and demonstrated a sister-group relationship with the Pygopodidae. Although Kluge (1987) did not specifically address the question of carphodactyline monophyly he did continue to list the tribe Carphodactylini as a (presumably natural) unit in the classification scheme isomorphic with his phylogenetic hypothesis. Although I accept Kluge's (1987) phylogenetic hypothesis I disagree with the ranks proposed for the clades in his classification. Specifically the inclusion of the subfamily Diplodactylinae with the Pygopodinae within the Pygopodidae disrupts the taxonomic stability of a large number of geckos and suggests a fundamental shift in the conception of both the Gekkonidae and the Pygopodidae. The relegation of pygopodids to subfamilial rank within the Gekkonidae would retain the current meaning of the two groups as well as maintain isomorphy. Kluge's (1987) statement that pygopodids may share additional derived characters with the Diplodactylini suggests that the rank of the flap-footed lizards may yet be even further reduced to that of a tribe.

King (1987a, 1987b, 1988) has used karyological and albumin immunological data to support the monophyly of the Diplodactylinae, but has proposed that the Carphodactylini should include the genus *Oedura*, which shares a derived karyomorph with the carphodactylines as presently construed. However, at least two species of *Oedura* as well as some *Nephrurus* and *Phyllurus* do not share the derived pattern and the basis for recognizing specific karyomorphic features as synapomorphies is not altogether clear.

I accept, for the present, the monophyly of the Carphodactylini on the basis of the preanal organ character proposed by Kluge (1967b) and accordingly base the determination of polarity by outgroup method on the hypothesis of higher order gekkotan relationships derived by Kluge (1967a, 1983a, 1987) and summarized in Fig. 3.
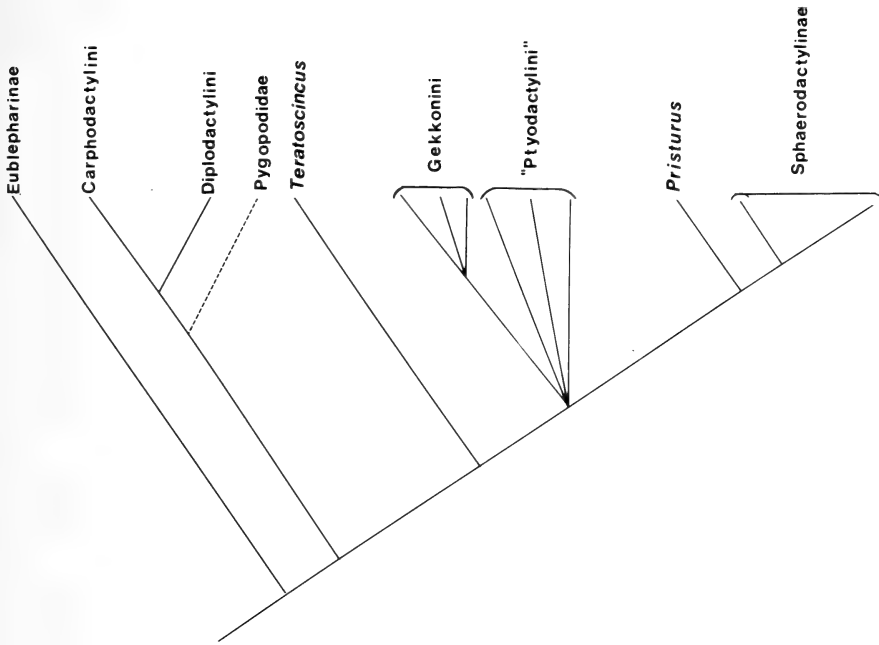
Fig.3: Hypothesis of higher order gekkonid relationships (after Kluge 1967a, 1967b, 1987) used in this analysis for the purpose of selecting outgroups. Dashed line indicates tentative placement of the Pygopodidae. For the purposes of this study all taxa from *Teratoscincus* to the right of the cladogram are considered to be Gekkonine geckos. Quotation marks around the Ptyodactylini indicate the recognized paraphyly of this taxon. The most commonly used taxonomic group names are used although these are not necessarily isomorphic with respect to the phylogeny.

MATERIALS AND METHODS

More than 3000 specimens (see Appendix B), representing all but one of the species of carphodactyline geckos, were examined including living and preserved material from major museums and a few private collections (see Appendix A for collection acronyms). Formalin or alcohol fixed specimens stored in 65-75% ethanol provided the basis for external character analysis. Many of these specimens, particularly those from New Caledonia, were collected during the course of the study. These animals were killed by intraperitoneal injection with T-61 euthanasia solution or by freezing before standard fixation with 10% neutral buffered formalin. Osteological information was obtained from dermestid beetle prepared dry skeletons or from specimens cleared and stained following a modification of the methods of Wassersug (1976), Dingerkus & Uhler (1977), and Hanken & Wassersug (1981). In addition, whole body radiographs of

representatives of most species were prepared for use in the study of post-cranial characters.

I employed the method of Hennig (1966) (= phylogenetic systematics) in order to deduce patterns of genealogical relationship among the carphodactyline geckos. The polarity of characters was generally assessed by outgroup comparison (Watrous & Wheeler 1981; Farris 1982; Maddison et al. 1984; Brooks & Wiley 1985) which appears to be the most philosophically robust and generally applicable method (P.F. Stevens 1980). In the case of several digital characters, however, an argument based on the internal consistency of functional units has been invoked, even though its results conflict with those of the outgroup method. It is crucial to recall that polarity assessment in outgroup analysis invokes parsimony; that is, the character state(s) present at the ingroup node, or first outgroup node (Maddison et al. 1984) is determined based on the minimization of steps to that node. This type of parsimony (descriptive parsimony, sensu Johnson 1982; methodological parsimony, sensu Kluge 1984) does not have logical hegemony in this (or any?) biological instance. It is, rather, an objective criterion for assessing character state polarities, or more generally for choosing among hypotheses.

When employed in this study, outgroups were chosen on the basis of the extensive work on the higher systematics of gekkotans carried out by Kluge (1967a, 1967b, 1974, 1983a, 1987). Specifically, the outgroups used, in order of decreasing proximity to the Carphodactylini, were the members of the tribe Diplodactylini, the members of the subfamily Gekkoninae (including the species currently placed in the Sphaerodactylinae), and the members of the subfamily Eublepharinae. While relationships within these groups are not necessarily well established (see Kluge 1983a; Joger 1985), their placement relative to one another is now generally accepted (Fig. 3).

Despite irrefutable evidence for the close relationship of geckos and pygopodids (Underwood 1957; Kluge 1976, 1987) these latter lizards were not used as outgroup taxa. One reason is the absence in these limbless forms of many of the characters which are variable among the carphodactylines. Missing data can be accomodated by most computer-based phylogenetic analysis programs, however, pygopodids are so aberrant (in many of the characters used in this study) as to shed little light on intra-tribal affinities. More importantly, however, is the question of their phylogenetic relationship to the other taxa. Since the work of Underwood (1957), pygopodids have generally been regarded as the sister group of geckos, but more recent work suggests that they are the sister group to all, or part of, the Diplodactylinae (Kluge 1987).

Character state polarities were assessed according to the guidelines of Maddison et al. (1984), and in order to insure global parsimony in the subsequent analysis the primitive states for each character were determined at the first outgroup node rather than at the ingroup node. Under the algorithm of Maddison et al. (1984), a single state at the outgroup node may be determined if the two most proximal branches share a common state (Fig. 4b), or if the first and third taxa relative to the ingroup share the same state (Fig. 4c) (or, of course, if the character state does not vary in the outgroup members). However, in cases where the first sister taxon differs in state from the next two distally (Fig. 4d), no polarity can be assigned. These characters were retained in the analysis
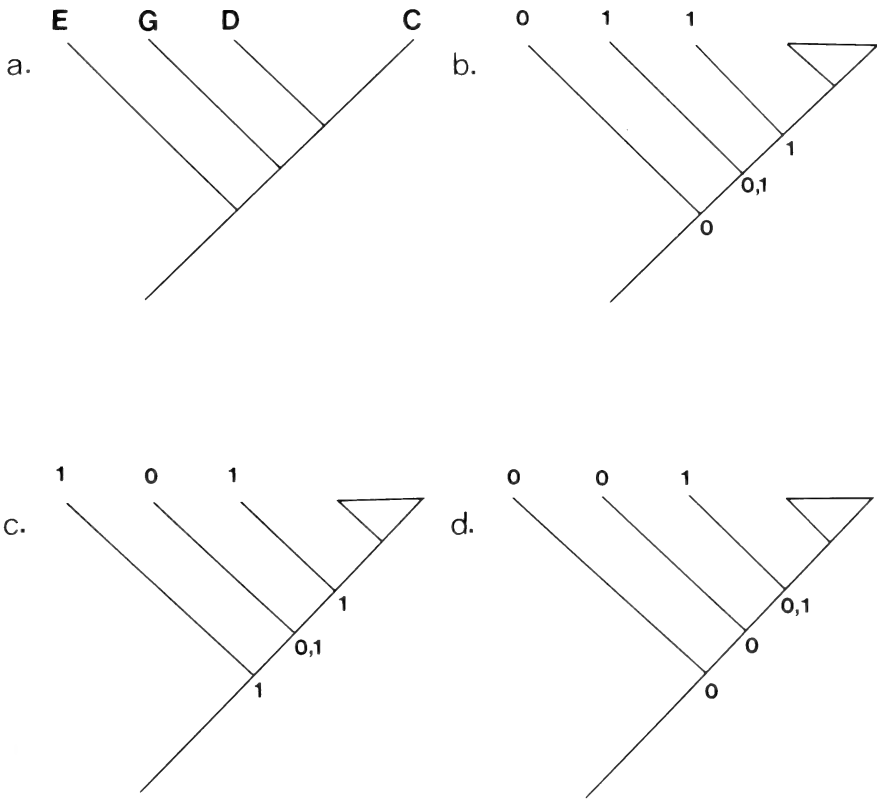
Fig.4: Method of assigning polarity by outgroup comparison (after Maddison et al. 1984).
a. Simplified cladogram of higher order gekkonid relationships (E= Eublepharinae, G= Gekkoninae, D= Diplodactylini, C= Carphodactylini).
b—d. Derivation of polarity at the outgroup (terminal) node resulting from the possible distribution of character states (0 or 1) in three successive outgroup taxa. See text for discussion.

but were entered as "missing" for the ancestor in the PAUP (Swofford 1985) analysis (see below) and were not, therefore, assigned polarity before the analysis. For the purposes of the analysis a hypothetical ancestral carphodactyline possessing the character states present at the outgroup node was assumed.

For the Diplodactylini and Eublepharinae, representatives of each genus were examined in order to supplement literature records for certain characters. The huge number of taxa in the Gekkoninae made a comprehensive survey impractical, but specimens of representatives of most major lineages as well as literature reports were used to determine the condition of this taxon.

Most species currently recognized as belonging to the carphodactylini were analysed (see species accounts). While some homogeneous subgroups exist, for example

Naultinus, generic monophyly has not been established for all carphodactylines and it was thus inappropriate to carry out a generic level analysis.

Procedurally I have assumed both the monophyly of the Carphodactylini as a whole and that of the OTU's, the individual species. The former requirement is, of course, necessary for the application of outgroup criterion. Thus, polarity determinants may shift in some characters if the ingroup is not monophyletic or if some members of the outgroup are actually members of the ingroup. The evidence for carphodactyline monophyly is admittedly weak. Kluge's (1967b) division of the Diplodactylinae is supported by several derived characters, most diagnosing the Diplodactylini, not the Carphodactylini. Nonetheless, Kluge's preanal organ patch character remains a putative synapomorphy for the tribe.

Some of the taxa analysed were actually complexes of several species — for example, *Bavayia cyclura* and *B. sauvagii* as run in the analysis each consist of several discrete biological entities. However, the complexes themselves are assumed to be monophyletic, thus there should be no affect on the results of the analysis.

Variation within single OTU's occurred in a number of presumptive characters. When this could not be attributed to pathology, sexual dimorphism or ontogeny, or when polarity could not be assessed within the taxon concerned, the character was discarded for the purposes of the analysis. Overall, few characters were involved, and most of these were variable for many taxa.

The character state distribution data were used to construct patterns of nested sets of taxa. Basal branches of these cladograms were initially constructed without computer aid, but the large number of taxa and degree of homoplasy in the data prevented resolution of distal branches by this method.

The patterns presented as cladograms were generated by the PAUP (Phylogenetic Analysis Using Parsimony) version 2.4 (Swofford 1985) on an IBM AT computer. This program uses the Wagner method (Kluge & Farris 1969; Farris 1970) to produce branching diagrams of minimal length.

A variety of options was used on the data set with varying degrees of success (both in terms of time to run and tree length). In general, however, the options MULPARS and SWAP = ALT with the default ROOT = ANCESTOR (refer to Swofford 1985) were most effective. Two data sets were run with this program. In both, taxa with a great deal of missing data were omitted. The taxa affected were *Rhacodactylus cavaticus, Hoplodactylus delcourti, H. kahutarae, H. chrysosireticus, Naultinus manukanus* and *N. tuberculatus*. The first species was not examined. The second is known only from a single mounted specimen. The remainder have been examined, but I lack skeletal information or have been unable to examine specimens in conjunction with comparative material. PAUP performs "Fitch optimization" (Fitch 1971) which treats missing data as "all possible states" and places the taxa on the tree in the most parsimonious way. Although the resulting placement of these taxa is probably little biased by the missing data, I chose to add these taxa (in tentative positions) after the initial analysis. The exclusion of these taxa does not result in distortion of the interpretation of relationships

among the remaining species (contra Arnold 1981). *Eurydactylodes symmetricus* was also excluded from the initial analysis as it shared the same character states for all characters with *E. vieillardi*.

The larger of the two sets run included all of the species level taxa except those listed above. A smaller data set was also run in which well supported, and largely homogeneous groups of taxa were reduced to a single "consensus" OTU. The collapsed taxa included all of the knob-tailed *Nephrurus*, all *Naultinus*, and all *Phyllurus*. The polarity of variable characters in the collapsed groups was reassessed on the basis of initial runs of the complete data set according to the algorithm of Maddison et al. (1984). Unpolarizable character states were rescored as missing in the "consensus" OTU.

In association with the reduced data set, each collapsed set of three or more taxa was reanalyzed by PAUP using the branch and bound method, with the ancestor designated as possessing the character states present at the outgroup node relative to the group. In the case of *Naultinus*, in which very few characters were variable, the run was aborted after more than 200 equally parsimonious trees (all of branch length 6) had been generated.

Finally, a consensus tree (Rohlf 1982) was prepared by hand from all of the trees generated. This process essentially involved the collapsing of conflicting branching patterns into polychotomies at the nodes in question. The resulting cladogram was ultimately used as a hypothesis of relationship within the Carphodactylini. Although this compromise tree is less explanatory than any of the original trees from which it is derived (Mickevich & Farris 1981; Farris 1983; Carpenter 1988) it does serve to highlight weak areas of the analysis and is here used in preference to other methods (e.g. Carpenter 1988) of choosing among multiple equally parsimonious cladograms.

CHARACTER ANALYSIS

A large number of skeletal characters was evaluated for all carphodactyline species available. When possible, character state distributions were supplemented by information from the literature. In addition to osteological characters, 46 characters of coloration and external anatomy and one character each dealing with reproductive mode and behavior were employed in the phylogenetic analysis. Each character is described in general for the Carphodactylini and variation within the tribe is assessed. Determination of character state polarities, if possible, is indicated. Character states are listed as 0 (primitive) or 1 (derived) based upon the condition possessed by the "ancestor" — i.e. the outgroup node (Maddison et al. 1984). Characters for which polarities could not be assessed initially are listed as A or B. The polarity of some of these characters was determined using the preliminary results of the PAUP analysis. Only when one or more successively nearer outgroups (relative to the taxa having the putatively apomorphic character state) were identified as a result of the primary analysis was this procedure employed. Thus, the polarity a character having the distribution illustrated in Fig. 4d,

which could not be assessed initially on the basis of the outgroup method (Maddison et al. 1984) could be determined by the addition of an additional, proximal sister taxon from within the Carphodactylini. In practice, this was possible when the character in question varied only within one of the two major lineages resulting from the analysis (see "Results"). The polarities of characters 9, 13, 16, 24, 29, 32, 33, 50, 54, 66, 79, 83 and 101 ultimately could not be determined. Historical and functional aspects of particular characters are presented when appropriate. A full character matrix is provided in Appendix C.

Cranial Osteology

Though lizard cranial osteology has been well studied in some forms (e.g. the Lacertidae, Parker 1880; Gaupp 1906; Brock 1935; DeBeer 1930, 1937; Bellairs & Kamal 1981), relatively little attention has been focussed on the gecko skull. Even this work, in general, has been restricted to the analysis of the elements of the skull in one or a few species. Wellborn (1933), in her review of comparative osteology, considered 20 species, but no carphodactylines were among them, and Grismer (1988) analysed cranial characters in the eublepharines. Other studies which compared several taxa include those of Häupl (1980) on five gekkonines, Stephenson & Stephenson (1956), and Stephenson (1960) on New Zealand and Australian forms respectively (the latter also includes information on New Guinea and Caribbean gekkonine species), and Cope (1892), Camp (1923), and Rieppel (1984a) on representatives of all four subfamilies. Kluge (1967a, 1967b, 1987) and Moffat (1973a) also discussed some cranial characters but made no attempt at complete descriptions of the skull. Descriptive works exist for *Coleonyx* (Kluge 1962), *Palmatogecko* (Webb 1951), *Afroedura* (Webb 1951; Cogger 1964), *Homonota* (Fabián-Beurmann et al. 1980), *Hemidactylus* (Mahendra 1949; Liang & Wang 1973; Fabián-Beurmann et al. 1980), *Uroplatus* (Siebenrock 1893) and *Oedura* (Cogger 1964). Aspects of developmental osteology and of the chondrocranium have been considered by Brock (1932), Kamal (1960, 1961a, 1961b, 1961c, 1965a, 1965b), El-Toubi & Kamal (1961a, 1961b, 1961c), Sewertzoff (1900) and Häfferl (1921). Pratt (1948) and Underwood (1957), among others, have discussed the gekkonid skull in papers dealing primarily with other lepidosaur groups.

The carphodactyline skull exhibits no major modifications or structural innovations relative to those of other gekkonids. It shows the typical gekkonid condition of the loss of the supratemporal arch. This feature has been considered a gekkotan synapomorphy by Kluge (1967a, 1987) as has the reduction of the jugal, which is responsible for the incomplete postorbital arch in this group (Underwood 1957; Kluge 1967a, 1987). The reduction of bracing structures in the gekkonid skull contributes to the internal mobility of the skull as a whole. The skulls of carphodactylines and all other geckos studied to date are amphikinetic (Webb 1951; Frazzetta 1962). Rieppel (1984a) discussed a number of trends in cranial anatomy associated with kineticism.

A basic description of each cranial element used in the analysis is given and specific characteristics that vary within the group are described for individual taxa. Many

elements are similar in shape and position throughout all geckos and, to avoid repetition, the reader is directed to Kluge (1962) and Grismer (1988) for descriptions of certain morphologically complex elements.

I have made no attempt to be exhaustive in the analysis of cranial features and their variation. Those of the neurocranium and occipital region, in particular, could not be examined in detail in many of the taxa due to a lack of disarticulated material. I examined, but found no significant or consistent variation in the following cranial elements of the species examined: maxilla, septomaxilla, prefrontal, vomer, palatine, pterygoid, epipterygoid, ectopterygoid, sphenoid, prootic, opisthotic, exoccipital, supraoccipital, basioccipital and stapes. Bauer (1986) provides detailed discussions of the shape and position of these bones among the carphodactylines.

Cranium — (Cranial features are illustrated by the skulls of *Nephrurus deleani*; *Rhacodactylus ciliatus* and *R. leachianus* in Figs. 5—7).

Co-ossification

Character 1: Dorsal skin of head free of skull (0) or co-ossified (1).

Co-ossification (character 1) involves the direct application of the dermis to the underlying bone. This condition is derived for carphodactylines as it is lacking in all species of the Diplodactylini. It was first noted in *Nephrurus* by Boulenger (1885a). Stephenson (1960) recorded co-ossification of the skull and skin in *Nephrurus* (except *N. milii*), *Phyllurus* and *Carphodactylus*. Kluge (1967b) recorded the trait as present in the last of these genera and in *Pseudothecadactylus* and scored it as variably present in *Nephrurus*, *Phyllurus* and *Rhacodactylus*. He also considered the likelihood of co-ossification in *Heteropholis* to be high, but did not record the condition in any of the specimens he examined. I have found co-ossification in specimens of the following taxa: *Nephrurus levis* (frontals — also reported for prefrontals, postfrontals and parietals, Stephenson 1960), *N. asper* (frontals, prefrontals, parietals, postfrontals, squamosals), *Rhacodactylus australis, R. leachianus* and *R. trachyrhynchus* (nasal process of premaxillae, nasals, maxillae, prefrontals, frontals, parietals), *Phyllurus cornutus, P. salebrosus* and *Carphodactylus laevis* (nasals, maxillae, prefrontals, frontals, postfrontals, parietals, squamosals), and *P. platurus* and *P. caudiannulatus* (all of the above mentioned elements except the squamosal). Cogger (1975a) stated that the skull of *Pseudothecadactylus lindneri* "is distinctly ornamented on the snout" but this was not confirmed by the specimens I examined. The distribution of co-ossification varies ontogenetically (Stephenson 1960) and neonates of all species (except perhaps *R. trachyrhynchus*) have unornamented skulls.

Premaxilla

Character 2: Premaxillae fused along midline with partial trace of suture (0) or with no remaining suture (1).

The premaxillae are dermal bones at the anteriormost extent of the snout. The body of each premaxilla forms the ventral or anterior border of the external naris and the
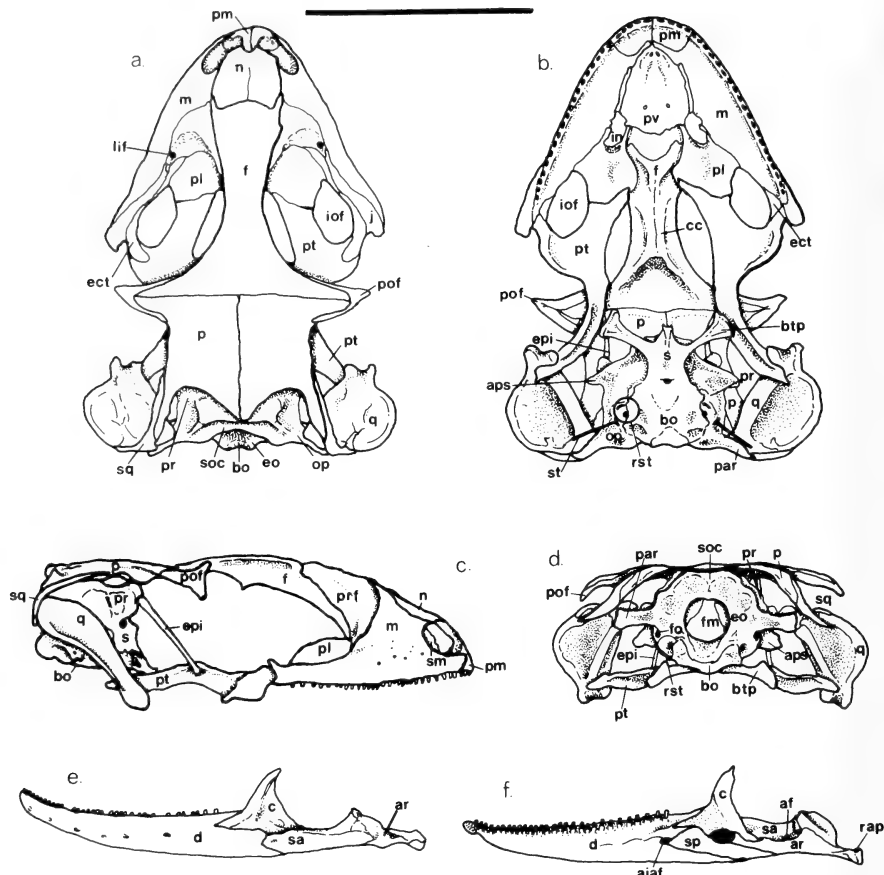
Fig.5: Views of the skull of *Nephrurus deleani* (AMB 46). a. dorsal, b. ventral, c. lateral, d. posterior, e. lateral view of mandible, f. medial view of mandible. Scale bar = 10 mm. The following list of abbreviations applies to Figs. 5—7.

af — adductor fossa
aiaf — anterior inferior alveolar foramen
amf — anterior mylchyoid foramen
aps — alar process of sphenoid
ar — articular
bo — basioccipital
btp — basitrabecular process
c — coronoid
cc — crista cranii
d — dentary
ect — ectopterygoid
eo — exoccipital
epi — epipterygoid
f — frontal

fo — fenestra ovalis
in — internal naris
iof — infraorbital fenestra
j — jugal
lif — lateral infraorbital foramen
m — maxilla
n — nasal
op — opisthotic
p — parietal
par — paroccipital process
pl — palatine
pm — premaxilla
pof — postfrontal
pr — prootic
prf — prefrontal

pt — pterygoid
pv — prevomer
q — quadrate
rap — retroarticular process
rst — recessus scalae tympanii
s — sphenoid
sa — surangular
sm — septomaxilla
soc — supraoccipital
sot — spheno-occipital tubercle
sp — splenial
sq — squamosal
st — stapes
tc — trabeculae communis
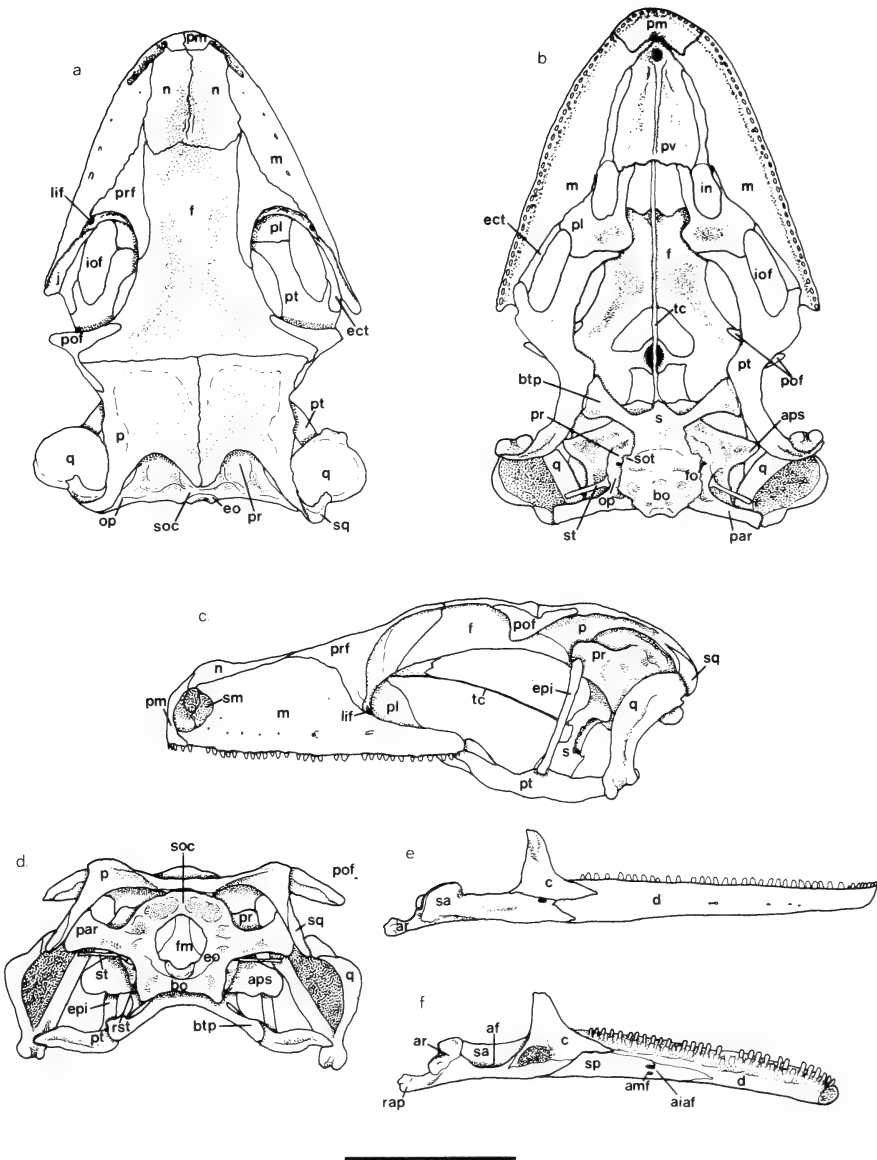
Fig.6: Views of the skull of *Rhacodactylus ciliatus* (BMNH 85.11.16.7). a. dorsal, b. palatal, c. lateral, d. posterior, e. lateral view of mandible, f. medial view of mandible. Scale bar = 10 mm. For abbreviations see Fig. 5.

nasal process of the premaxilla contributes to the medial border of the naris. A short, wide basal process is symplesiomorphic for the Carphodactylini (Kluge 1967b). Laterally and ventrally the body and pars dentalis of the premaxilla, respectively, contact the maxilla. Posteriorly the nasal process overlaps the paired nasals. The small septomaxilla abuts the pars dentalis dorsal to the palate.

The partially paired condition of the premaxillae observed in the Eublepharinae and Diplodactylinae is primitive for the family (Camp 1923; Kluge 1967a). In all carphodactylines the bones remain paired early in ontogeny (Kluge 1967a) although partial fusion occurs at the midline in species of *Hoplodactylus, Rhacodactylus, Bavayia, Naultinus* and *Eurydactylodes* by the time of parturition or hatching. Stephenson (1960) stated that the premaxillae were distinctly paired in the New Zealand taxa, but partial fusion characterized all of the postnatal specimens examined in this study; Kluge (1967b) stated that the premaxillae remained paired in *Eurydactylodes* and in *Pseudothecadactylus*, but this could not be confirmed. The bones remain paired throughout life with no fusion in the remaining Australian genera (character 2). Prehatchlings typically bear a single large deciduous egg-tooth on each premaxilla, as in the Diplodactylini and Eublepharinae. This condition is primitive for the Carphodactylini. However, as noted by Kluge (1967a), the live-bearing species of New Zealand geckos show no such structures and the adult-type dentition is present on the pars dentalis at birth. The condition in the live-bearing New Caledonian species *Rhacodactylus trachyrhynchus* requires study. In the youngest specimen available to me (less than one month post-natal), adult dentition is present. Hatchlings of *R. auriculatus, R. chahoua* and *R. leachianus* all conform to the typical, plesiomorphic condition. The states of this character are thus coincident with those for reproductive mode (see character 106).

Nasal

Character 3: Nasal bones short and relatively broad (0) or elongate and narrow (1).

The nasals are roofing bones lying just dorsal and posterior to the external nares. The nasals are paired in all carphodactylines and are azygous only in a small number of gekkonines (Kluge 1967a). Anteriorly they are partially covered by the overlapping nasal processes of the premaxillae. Laterally they border the ascending plates of the maxillae to the border of these elements with the frontal, which is overlapped by the posterior portion of the nasal. The nasals are generally similar amongst all geckos. In most species they are relatively short and wide; however, an apomorphic condition of elongate, somewhat narrowed nasal bones is typical of *Carphodactylus laevis* and the species of *Phyllurus* (character 3).

Frontal

Character 4: Frontal bone much longer than wide (0) or approximately as wide as long (1).

Character 5: Supraocular portion of frontal generally flat (0) or deeply furrowed or concave (1).

The frontal is the most extensive dermal roofing bone. It is invariably azygous in diplodactylines. It is bounded anteromedially by the overlapping nasals and anterolaterally by the prefrontal. Kluge (1967b) recorded a variety of character states for maxilla/frontal contact within the Carphodactylini. Based on the condition seen in the Diplodactylini (Kluge 1967b; Cogger 1964), contact would appear to be derived. However, in the secondary outgroup, the Gekkoninae, this state appears to be general (Wellborn 1933; Häupl 1980) as it does in the Eublepharinae (Kluge 1962). Extensive contact is rare among the carphodactylines and has been reported only for *Carphodactylus, Pseudothecadactylus* and *Bavayia* (Kluge 1967b). Contrary to these reports I found that maxilla/frontal contact was typical only of *Nephrurus sphyrurus*. In other species a narrow anterior process of the prefrontal or the body of the prefrontal itself provides a narrow separation between the two elements. In several other species contact was variable among specimens, and in *Hoplodactylus duvaucelii* contact appears to increase with body size. Given the extreme variability of this character within the basic taxa of this study I consider it uninformative at this level of analysis.

The frontal forms the dorsal ridge of the orbit and runs posteriorly to the transverse frontoparietal border where it contacts the small postfrontals laterally. Ventrally the thickened supraorbital ridges form an enclosed passage (the crista cranii) through which cranial nerve I passes on its way to the telencephalon. Rieppel (1984c) indicated that these processes fuse without a trace of a suture in all gekkonids. The complete closure of this canal has been recognized as a synapomorphy of the Gekkota (Kluge 1967a, 1987).

On the basis of the condition in Diplodactylini, Gekkoninae and Eublepharinae, the frontal is primitively somewhat hour-glass shaped — longer than wide, with the widest point at the parietal suture. This condition obtains in all taxa except the knob-tailed *Nephrurus*. In this group the posterior portion of the frontal is widened to almost the length of the element (character 4).

In the smooth knob-tail geckos, the midportion of the frontal is greatly narrowed, enhancing the apparent size of the orbits. This supraocular portion of the frontal is flat or nearly so in the Diplodactylini and the successively more distant sister taxa and is thus regarded as primitive for the Carphodactylini. This is the condition seen in *Naultinus, Nephrurus, Bavayia, Eurydactylodes, Hoplodactylus* (except in adult *H. duvaucelii*), *Phyllurus platurus* and *P. caudiannulatus*. A distinctive median groove or furrow is located medially in the frontal bones of *P. cornutus* and *P. salebrosus* as well as in *Carphodactylus* and *Rhacodactylus* (including *Pseudothecadactylus*) (character 5). The condition is most pronounced in *R. auriculatus* and is least developed in *R. trachyrhynchus* and the species of the subgenus *Pseudothecadactylus*.

Postfrontal

Character 6: Lateral prong of postfrontal extends horizontally or only slightly downcurved (0), or distinctly ventrally curved (1).

The postfrontal in carphodactylines is stirrup-shaped and articulates with the frontal and parietal. Although Camp (1923) and most subsequent workers have regarded the

bone as simple, some authors (e.g. Stephenson & Stephenson 1956; Rieppel 1984a) maintain that it contains both postfrontal and postorbital components. According to Rieppel (1984c) the postfrontal acts as a lateral brace for the otherwise highly kinetic frontoparietal joint. An elongate, blunt-ended process projects ventrolaterally to form the posterodorsal border of the orbit. The shape of the postfrontal is general for car-phodactylines but also occurs in several other gekkonid lineages (Häupl 1980). In *Uroplatus fimbriatus* the lateral prong of the element is extremely elongate and, as in some carphodactylines, it is connected to the mandible by a calcified postorbital liga-ment. In most species the element changes shape ontogenetically. Initially the limbs of the postfrontal are narrow and the bone as a whole is "y"-shaped. With age the limbs thicken and broaden and the element becomes more "v"-shaped. Primitively in the Car-phodactylini the lateral limb of the postfrontal curves somewhat downward as it does in many of the members of the outgroups. In *Rhacodactylus auriculatus* and *R. leachianus*, however, the process is so downcurved as to be oriented nearly vertically (Fig. 7) (character 6).
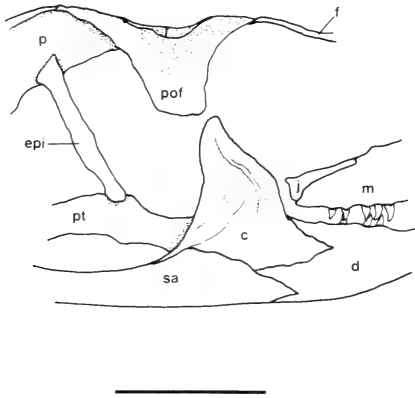
Fig.7: Lateral view of the postorbital region of the skull of *Rhacodactylus leachianus* (CAS 165890) showing greatly downturned postfrontal approaching the coronoid (character 6). Scale bar = 10 mm. For ab-breviations see Fig. 5.

Parietal

Character 7: Posterior border of parietals distinctly emarginate (0), or complete — roofing entire occipital region (1).

Character 8: Parietals as a unit approximately as long as wide (0), or short and very wide (1).

Character 9: Frontoparietal suture straight (A), or curved (B).

Character 10: Parietal crest at mid-dorsal suture absent (0), or present (1).

The parietals are the posteriormost roofing bones of the skull. The paired condition shared by all diplodactylines has been considered both primitive (Moffat 1973a) and derived (Kluge 1967a) for gekkonids, although there seems little support from outgroup comparison for the former view. Stephenson (1960) reported partial fusion of the parietals in *Carphodactylus laevis*. While I could not confirm this observation, I did

find that virtually complete fusion of the parietals had occurred in adult *Rhacodactylus leachianus* and in both adult and juvenile *R. trachyrhynchus*. Similarly, the radiographs of *Hoplodactylus delcourti* show no sutures. This character is taken to be uninformative in terms of phylogenetic reconstruction; it is regarded as a byproduct of the gigantic size attained by all of these species of geckos.

Anteriorly, the parietal contacts the frontal and the posterior limb of the postfrontal. Posteriorly, lateral processes of the parietals contact the squamosal ventrolaterally. Ventrally, the parietals abut the supraoccipital at the midline. In the primitive condition the lateral posterior processes of the parietal curve anteromedially, producing an emargination bounded medially by the supraoccipital tubercle. A caudal extension of the parietal plate has reduced or eliminated this emargination in *Phyllurus, Carphodactylus* and in *Nephrurus asper* and *N. levis* (character 7). In all members of these genera the parietal is greatly broadened and shortened as compared with the primitive state (character 8). These genera also share with *Rhacodactylus* and *Pseudothecadactylus* a straight, rather than curved, frontal suture (character 9). The polarity of this trait cannot be assessed on the basis of available evidence. A small median parietal crest is a derived feature typical of *R. auriculatus* and *R. ciliatus* (character 10). *Rhacodactylus trachyrhynchus* is autapomorphic in its possession of an extremely elongate parietal.

Squamosal

Character 11: Squamosal small and splint-like (0), or large and relatively broad (1).

The squamosal is typically a relatively small element lateral to the parotic process and parietal and in contact with the postero-medial aspect of the quadrate. Camp (1923) considered the element the tabulare (= supratemporal bone), based on analogy with *Heloderma*. Brock (1935) also supported this view and Bellairs & Kamal (1981) considered it the prevailing interpretation through the 1950s. Underwood (1957), however, located a tiny supratemporal element between the so-called tabulare and parietal in the Eublepharinae and thus established the element in question as the squamosal. Kluge (1962, 1967a) provided additional evidence for this interpretation that has led to its subsequent widespread acceptance (Rieppel 1984b), although Häupl (1980) referred to the element simply as the "Temporalknochen".

Dorsally the thin, laterally-oriented blades of the squamosal articulate with the posterior process of the parietal. Posteriorly and ventrally it curves to lie medial to the dorsal portion of the quadrate conch and lateral to the anterolateral face of the paroccipital process. The squamosal is greatly expanded in *Nephrurus asper, Carphodactylus laevis* and *Phyllurus* (character 11) and participates in the formation of the dorsal skull roof. This expansion represents a derived condition.

Quadrate

Character 12: Lateral lip of quadrate narrow (0), or expanded as a lateral flange (1).

The quadrate is a large bone lying lateral to the brain case and participating in the jaw articulation. Dorsomedially, the quadrate contacts the squamosal and the paroccipital process of the opisthotic. Ventrally, the quadrate condyle articulates with a groove in

the articular bone of the mandible. The posterior projection of the pterygoid contacts the medial portion of the condyle above the jaw articulation. In posterior view, the quadrate above the condyle is greatly concave, forming the quadrate conch. The medial edge of the conch is thickened and more or less straight. The lateral border of the conch is generally curved or slightly flared. A derived condition in which the lateral borders are broadly flared is seen in *Rhacodactylus ciliatus* and *R. auriculatus* (character 12) (see Fig. 6).

Jugal

Character 13: Overlap of jugal and lateral infraorbital process of prefrontal extensive A) (0), or narrow or excluded B) (1).

The jugal in carphodactylines is a bony splint dorsal to the maxillary shelf, which lies between the lateral wall of the maxilla and the ectopterygoid. Anteriorly, within the border of the orbit, the jugal contacts the infraorbital process of the prefrontal. Kluge (1967b) considered the jugal long and wide in all carphodactyline genera except *Bavayia* (moderately long and narrow) and *Eurydactylodes* (not recorded). However, I found variations within taxa to be great in the present study and no discrete character states could be assigned. Extensive overlap of the jugal by the lateral infraorbital process of the prefrontal (Kluge 1967b) is seen in *Hoplodactylus* and *Rhacodactylus*, whereas the remaining genera show degrees of lesser contact from "nearly touching" *(Bavayia)* to "some overlap" (Kluge 1967b) (character 13).

Basioccipital

Character 14: Recessus scalae tympani exposed ventrally A) (0), or at least partially obscured in ventral view by lateral process of the basioccipital B) (1).

The basioccipital forms the posterior portion of the floor of the brain case. Anteriorly, it contacts the sphenoid. Posteriorly the basioccipital narrows to form the thickened, u-shaped lip of the ventral border of the foramen magnum. Laterally it contacts the prootics, opisthotics and, posterolaterally, the exoccipital. Anterolaterally the basioccipital contributes to the ventrally inflected spheno-occipital tubercle. Dorsal to the tubercle lies the recessus scalae tympani. In all *Rhacodactylus* there is a prominent lateral process of the basioccipital which, in ventral view, hides the recessus. This is a derived condition that is also present, though variably developed, in *Eurydactylodes* and *Bavayia* (character 14).

Scleral Ossicles

Character 15: 30 or more scleral ossicles (0), or fewer than 30 scleral ossicles (1).

Scleral ossicles are small plates of ossified cartilage that lie within the sclera of the eyeball in many amniotes, as well as certain anamniotes (Edinger 1929). It is generally thought that the ossicles maintain the shape of the eyeball (Walls 1942; de Queiroz 1982) although it is unclear how they function in this capacity given that they are absent in many major amniote groups, e.g. mammals, snakes and modern crocodilians. Under-

wood (1954) suggested that the reduction of the scleral sulcus in nocturnal geckos might reduce the functional significance of scleral ossicles even further.

Kluge (1967a) recorded scleral ossicle number for approximately 250 species of geckos, including members of most recognized genera. Outgroup information within the Gekkonidae for this character is derived chiefly from this data set. While the pattern of ossicle overlap may be of phylogenetic significance in some groups (de Queiroz 1982), it varies widely and may be difficult to score accurately in geckos (Underwood 1970, 1977a). Consequently only scleral ossicle number is considered here. It is problematical whether the mean species values or ranges should be used as character states. For the sake of convenience I have chosen to use mean values, although ranges are also reported. Eyes were removed from the sockets and manually cleared of the conjunctiva before counting. No stains were used.

Gugg (1939) and Underwood (1954) stated that 14 is the "standard" number of ossicles for amniotes. The view that 14 ossicles is also primitive for lepidosaurians and gekkotans was also espoused by Underwood (1954) and later endorsed by Moffat (1973a). Kluge (1967a), however, rejected 14 scleral ossicles as being primitive for geckos, citing the higher number found in eublepharines, especially *Aeluroscalobotes*, which he considered to be the most primitive living gecko. Data from outgroups provided by Underwood (1970) and de Queiroz (1982) clearly demonstrate that the former opinion is correct, and this view has since been accepted by Kluge (1987). The primitive condition for carphodactylines, however, would appear, on the basis of immediate outgroup analysis, to be the presence of a high number of scleral ossicles. Among the Diplodactylini Kluge (1967a) reported mean ossicle numbers of less than 30 in only two of 25 species and the overall species mean for this group is 32.7, ranging as high as individual counts of 40 in *Diplodactylus conspicillatus* (the highest number known for any vertebrate). This character is scored as derived for the Carphodactylini if mean species ossicle number is less than 30 (character 15).

The scleral ossicle counts for all carphodactylines examined are presented in Table 2. Means range from 20.5 to 35.3. Variation is high in most species with high sample size, but no sexual or ontogenetic trends in variation have been noted. My data do not support Stephenson's (1960) claim that ossicle number decreases with age in *Nephrurus*.

Mandible

The lower jaw consists of five discrete elements in the Carphodactylini. Features of the mandible are illustrated in Figs. 5 and 6 for *Nephrurus deleani* and *Rhacodactylus ciliatus*. No consistent patterns of variation were noted in the dentary splenial, coronoid, or articular bones.

Surangular

Character 16: Surangular dentary suture at the same antero-posterior position as coronoid-dentary suture A), or posterior to coronoid-dentary suture B).

Much of the posterior portion of the mandible, including both medial and lateral faces, is formed by the surangular. Laterally it is overlapped by the posterior processes of the

T a b l e 2. Scleral Ossicle Counts for Species of Carphodactyline Geckos.

Taxon	n (eyeballs)	No. of Ossicles Range (Mean)	Source
Bavayia cyclura	8	29—33 (31.7)	B, K, U3
Bavayia sauvagii	18	30—34 (32.0)	B, K
Carphodactylus laevis	6	30—33 (31.2)	K, S
Eurydactylodes vieillardi	3	26—27 (26.7)	B, K, K2
Hoplodactylus duvaucelii	8	24—26 (25.0)	B, K, (SS)
Hoplodactylus granulatus	10	23—27 (25.4)	B, K
Hoplodactylus maculatus	4	26—28 (27.0)	B, (K*)
Hoplodactylus pacificus	?	25**	(U, SS)
Hoplodactylus stephensi	1	24	B
Nephrurus asper	8	28—33 (30.4)	B, K, (S)
Nephrurus deleani	4	32—33 (31.8)	B
Nephrurus laevissimus	6	31—35 (32.7)	B, K
Nephrurus levis	18	32—39 (34.3)	B, K, (S)
Nephrurus milii	20	28—31 (29.4)	K, (S)
Nephrurus sphyrurus	4	27—29 (29.4)	B, K
Nephrurus stellatus	1	29	B
Nephrurus vertebralis	1	31	B
Nephrurus wheeleri	2	32—33 (32.5)	K
Phyllurus caudiannulatus	1	26	B
Phyllurus cornutus	4	25—27 (26.0)	K
Phyllurus platurus	12	24—28 (26.0)	B, K, (S, SS)
Phyllurus salebrosus	2	28—30 (29.0)	B
Naultinus elegans	10	18—23 (20.9)	B, K, U, (SS)
Naultinus grayii	2	20—21 (20.5)	B
Naultinus tuberculatus	2	21—22 (21.5)	K
Rhacodactylus auriculatus	16	27—31 (28.8)	B, K, (U2+)
Rhacodactylus australis	2	31—32 (31.5)	K
Rhacodactylus chahoua	4	33—36 (34.0)	B
Rhacodactylus ciliatus	1	32	B
Rhacodactylus leachianus	3	28—29 (28.6)	B
Rhacodactylus lindneri	3	35—36 (35.3)	B
Rhacodactylus sarasinorum	1	35	B
Rhacodactylus trachyrhynchus	1	33	B

References: B — Bauer, this study; K — Kluge (1967a); K2 — Kluge (1967b); S — Stephenson (1960); SS — Stephenson & Stephenson (1956); U — Underwood (1954); U2 — Underwood (1970); U3 — Underwood (1977a). Sources appearing in parentheses provided ossicle numbers but not sample sizes and consequently are not represented in the ranges or means.

*   — Kluge (1967a, 1967b) did not recognize the species *H. maculatus*, therefore his values for *H. pacificus* may include (or consist entirely of) *H. maculatus*. For this reason the figures reported by Kluge have not been included in the table.

**   — Neither source provides a sample size.

+   — Underwood (1970) reported counts of 26 and 27 for *Rhacodactylus*, but did not specify the species. It is likely that these figures refer to *R. auriculatus*.

dentary and coronoid, while medially it contacts the dentary and coronoid anteriorly and the articular ventrally and posteriorly, enclosing the mandibular fossa. Two patterns of surangular position are seen on the lateral face of the mandible in carphodactylines. In *Nephrurus, Carphodactylus* and *Phyllurus* the anterior-most border of the surangular lies posterior to the anterior-most lateral border of the coronoid. In all other species the borders of the two elements lie approximately at the same level (character 16). This character varies in the outgroups and no assessment of polarity could be made.

Teeth

Character 17: Teeth moderate to small (0), or extremely minute (1).

Adult gekkonid teeth are generally conical, homodont and pleurodont and are borne on the lingual faces of the dentary, maxilla and premaxilla. The number of teeth in post-hatchlings has been demonstrated to vary greatly within species (Kluge 1962; Bauer & Russell in press). An increase of tooth number with age corresponds to an increase length of the germinal tooth region. In adult geckos, as in other lizards, the number of teeth tends to vary around a particular species mode (Owen 1866). Except for *Teratoscincus*, in which teeth in the middle of the tooth rows are the longest (Edmund 1969), teeth tend to increase in size anteriorly in geckos. Among eublepharines and diplodactylines, and primitively in gekkonines, teeth are of moderate size and are relatively blunt and somewhat compressed distally. This morphology is characteristic of most carphodactylines (Fig. 8b). However, all *Nephrurus, Carphodactylus* and *Phyllurus* possess tiny, extremely numerous teeth similar in shape to those of other geckos (Fig. 8c) (character 17). Elsewhere amongst geckos this morphology appears in *Uroplatus*. Interestingly, *Hoplodactylus delcourti* and *Rhacodactylus leachianus*, which share gigantic size with *Uroplatus fimbriatus*, show rather typical tooth counts for their respective genera. There are no obvious functional correlates of this derived morphology. These geckos are more or less typical in their diet, except that *Nephrurus* frequently take vertebrate prey items (Pianka & Pianka 1976; Pianka 1986). A second derived morphology occurs in *Rhacodactylus auriculatus*. This gecko possesses elongate, slender, pointed teeth (Fig. 8a). Again the significance of this morphology is unclear but may be related to the vertebrate prey taken by this species (Bauer & DeVaney 1987; Bauer & Russell in press). Cuspation patterns vary with some phylogenetically
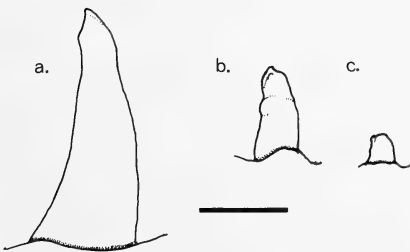
Fig.8: Anterior maxillary teeth of (a) *Rhacodactylus auriculatus* (CAS 165891), (b) *Hoplodactylus duvaucelii*, juvenile (AMB 455) and (c) *Nephrurus deleani* (AMB 46). Note the small size of tooth c (character 17) and the elongate fanglike structure of a. Scale bar = 0.5 mm.

significant patterns amongst other gekkonids (Sumida & Murphy 1987) and may be expected to do so in the Carphodactylini, although this type of variation was not assessed in the present study.

Hyobranchial Apparatus

Character 18: Hyoid cornu with both anteromedial and posterolateral processes well developed (0), or with anteromedial process reduced and posterolateral process large, hooked (1).

Character 19: Inner promixal ceratohyal process absent (0), or present (1).

Character 20: Second epibranchial short, moderately to widely separated from second ceratobranchial (0), or long and recurred, nearly in contact with cerabranchial (1).

Camp (1923) emphasized the importance of the hyobranchial apparatus by assigning the greatest "paleotelic" weight (i.e. indication of primitiveness) to a character of this
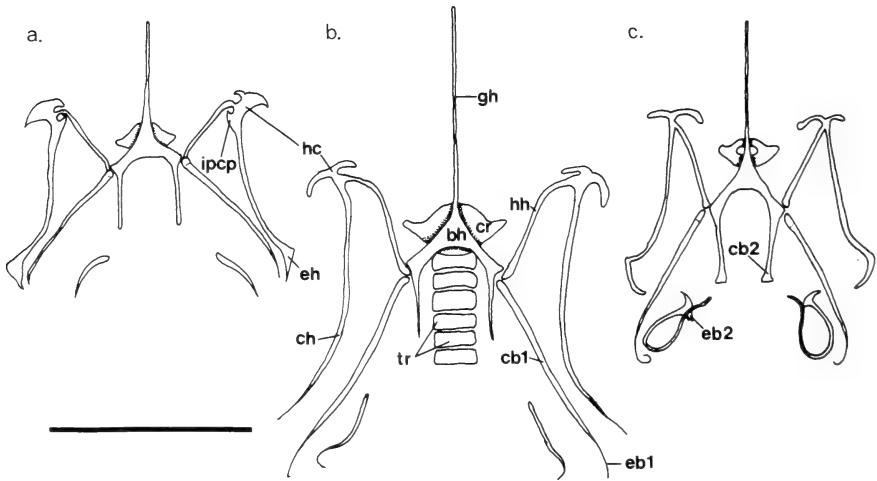
Fig.9: Hyoid apparati of representative carphodactyline geckos. (a) *Nephrurus laevissimus* (LACM 57101), (b) *Rhacodactylus auriculatus* (CAS 165895) and (c) *Bavayia sauvagii* (CAS 165905). Note the overlap of the second epibranchials in c (character 20), the shape of the hyoid cornu (character 18) and the presence of the inner proximal ceratohyal process in a. Scale bar = 10 mm. Abbreviations are as follows:

bh — basihyal	eb1 — first epibranchial	hh — hypohyal
cb1 — first ceratobranchial	eb2 — second epibranchial	ipcp — inner proximal
cb2 — second ceratobranchial	eh — epihyal	ceratohyal process
ch — ceratohyal	gh — glossohyal process	tr — tracheal cartilages
cr — cricoid cartilage	hc — hyoid cornu	

structure (the number of complete branchial arches). Following Fürbringer (1919) and Noble (1921), Camp and later authors (e.g. Stephenson & Stephenson 1956; Kluge 1967a) accepted that the complete arch arrangement first illustrated in *Coleonyx* by Cope (1892) was plesiomorphic. Kluge (1983a), however has demonstrated that the presence of three uninterrupted arches (the hyoid plus branchial arches I and II) are derived reversals occurring in *Coleonyx* spp. among eublepharines and *Gonatodes vittatus* in the sphaerodactylines. Stephenson & Stephenson (1956) reported the same condition in the carphodactyline *Naultinus elegans*. However, I was unable to confirm this observation in any of the *Naultinus* examined in the course of this study.

The typical carphodactyline hyobranchial apparatus (Fig. 9) consists of a central tripartate basihyal extending anteriorly into a narrow glossohyal process, lying ventral to the cricoid cartilage of the larynx. The hypohyals run anterolaterally from the dorsal margin of the posterior apices of the basihyal and fuse with the posterolaterally-directed ceratohyals at the hyoid cornu, a wing-like process lateral and just anterior to the level of the cricoid. The cornu varies in form among gekkonines (Wellborn 1933) but is relatively uniform in the Carphodactylini. However, all *Carphodactylus, Nephrurus* and *Phyllurus* exhibit a uniquely derived morphology of the cornu in which the anteromedial prong is reduced and the posteriolateral prong is drawn out into a broad, blade-like process (Fig. 9a) (character 18). An inner proximal ceratohyal projection was reported by Kluge (1967a) in *Carphodactylus, Nephrurus, Phyllurus* and *Naultinus* (character 19). This feature is absent in the Diplodactylini and the Eublepharinae and variable present in the Gekkoninae (including the Sphaerodactylinae). Its presence in certain carphodactylines is interpreted as being derived. A small, medially curving epihyal is fused to the posterior tip of the ceratohyal and abuts the paroccipital process of the cranium. The fusion of the distal portion of the ceratohyal with the crista parotica of the auditory bulla recorded in certain geckos (Versluys 1903; Brock 1932) is not seen in any carphodactyline.

The first ceratobranchial extends posterolaterally from the basihyal and terminates in a small hooked epibranchial. This arch is not associated with the cranium and may continue posteriorly for a considerable distance in the throat musculature. It is exceedingly elongate in *Rhacodactylus leachianus* where it may extend past the level of the fourth cervical vertebra. The second branchial arch (visceral arch four) consists of paired posteriorly projecting ceratobranchials fused to the basihyal and medially-looping epibranchials. As previously mentioned, there is a definite break between these elements in all carphodactylines, although both elements are invariably present. However, in gekkonines, the second ceratobranchial is variably present, and Kluge (1983a) has used the presumed synapomorphy of the loss of the second ceratobranchial as the sole character supporting his division of that subfamily into two tribes. While no carphodactyline shows the complete arch, the gap between the epi- and ceratobranchials is very small in *Bavayia* (Fig. 9c). Members of this genus also show another condition interpreted as derived on the basis of outgroup comparison; the second epibranchial curves in a circle, terminating in a flanged tip just dorsal to the gap separating its proximal end from the ceratobranchial (character 20).

Generally only the basihyal, glossohyal (or entoglossal) process, first and second ceratobranchials and part of the hypohyals ossify in adults. Additional ossification is seen in larger, older specimens of the larger species and, as in many osteological characters, *Naultinus* shows relatively little ossification in the hypobranchial apparatus.

Variation in the larynx and tracheal rings was not assessed but the basic morphology generally follows that reported by Kluge (1962) for *Coleonyx* and Mahendra (1947) for *Hemidactylus flaviviridis*.

Axial Skeleton

Vertebral Shape

Character 21: Trunk vertebrae amphicoelous (0), or procoelous (1).

Noble (1921) and Camp (1923) accepted amphicoely as primitive for lizards on "comparative grounds". Camp (1923) provided a discourse on the differences between procoely and amphicoely but no justification for his determination of polarity. Underwood (1954) and Romer (1956) considered the amphicoelous condition of gekkonid vertebrae to be secondarily derived although Underwood (1955) later reversed the polarity of this character on the evidence of amphicoely in kuehneosaurs, which he accepted as early lizards. Holder (1960) also accepted evidence from kuehneosaurs as supportive of primitive amphicoely in gekkotans. Her support from Mahendra's (1950) comparison of amphicoely in *Sphenodon* is uninformative with respect to the condition in geckos. Although she stressed the simplicity of a morphological transformation between the two types, Holder (1960) seems to have ruled out, a priori, the occurrence of paedomorphosis (in what she recognized as a generally paedomorphic group) to account for the amphicoelous condition in geckos. She also accepted Camp's (1923) relative assessments of paleotelic weight as inviolate; thus her arguments regarding the polarity of this character are circular.

Kluge (1967a) interpreted amphicoely as derived within gekkonids, citing the procoelous ardeosaurs as potential gekkotan ancestors. He also pointed out that kuehneosaurs, so important for the arguments of Underwood (1955) and Holder (1960), were not early lizards (see Evans 1982; Estes 1983). He further advocated a paedomorphic origin for the derived condition on gekkotan amphicoely. This is supported by the presence of persistent, and often unconstricted, notochord in the centra of adult geckos (Holder 1960; Moffat 1973a, 1973b; Werner 1961a, 1967, 1971; Hoffstetter & Gasc 1969). I accept this hypothesis as the most plausible explanation of the origin of this character state.

Procoely has apparently been derived independently in a number of gekkotan lineages including the Sphaerodactylinae (Noble 1921) and the Pygopodidae (Camp 1923; Stokley 1947), as well as in certain carphodactylines (Holder 1960; Kluge 1967a; Moffat 1973a). Kluge (1987), following Winchester & Bellairs (1977), stressed that condylar formation is essentially the same in geckos as in other squamates (contra Hoffstetter & Gasc 1969 and Werner 1971). Hecht (1976) and Hecht & Edwards (1977) interpreted Moffat's (1973a, 1973b) work on joint capsules as implying four character states of

"coely" and came to the conclusion that procoely was primitive for gekkotans. Based on parsimony arguments, Underwood (1977b) also returned to his 1954 stance on the question.

Despite his criticisms of Moffat (née Holder) (Holder 1960; Moffat 1973a), Kluge (1987) has recently accepted her assessment of amphicoely as primitive for gekkonids. In Kluge's scheme it would be equally parsimonious on other grounds to accept either state as primitive. His decision thus seems predicated on his acceptance of the Bavarisauridae (but not the Ardeosauridae) as the sister group of the living gekkotans. I disagree with this interpretation on the grounds that these groups are neither diagnosable nor share any derived features with living gekkotans and I accept procoely as primitive in the Eublepharinae and some ardeosaurs. Secondary procoely is characteristic of the pygopodids and sphaerodactylines. It is interesting to note that both lineages are typified by miniaturization (Rieppel 1984a) and it seems possible that acceleration (Gould 1977; Alberch et al. 1979), which has been suggested as being responsible for a number of skull features, may account for this condition.

Within the Carphodactylinae it is most parsimonious to view amphicoely as primitive. Thus procoely in *Carphodactylus laevis* and *Phyllurus milii* (Holder 1960; Kluge 1967a) is a derived condition (character 21).

Vertebrae and Ribs

The typical gekkonid presacral vertebra is relatively short and broad. This is generally true of all of the carphodactyline species. Twenty-four presacral vertebrae appears to be the primitive number for lizards as a whole and this number is frequently encountered in non-chameleontid iguanians (Romer 1956; Hoffstetter & Gasc 1969). The total number of presacral vertebrae varies between 23 and 29 within the gekkonids (Wellborn 1933; Hoffstetter & Gasc 1969), with 26 as a mode. Hoffstetter & Gasc (1969) remark on the "stabilization" at this number in most non- anguimorph scleroglossans. Members of the Diplodactylini have between 25 and 27 presacrals (Holder 1960), again with a mode at 26.

Among the species examined, presacral counts ranged from 24 to 27 (see Tab. 3). Holder (1960) examined a number of carphodactyline species and obtained similar results, although I found 26 rather than 27 vertebrae in all of the fifteen *Carphodactylus laevis* examined. Holder (1960) also found more variation in presacral vertebral number than I did, although her sample sizes, except for *Phyllurus platurus*, were smaller.

Cervical Vertebrae

There are generally eight cervical vertebrae in lizards (Romer 1956; Hoffstetter & Gasc 1969) and this is invariant in the Carphodactylini. The general morphology of the atlas and axis is not significantly different from the condition detailed in the eublepharine *Coleonyx* (Kluge 1962). Other detailed observations on the morphology of the adult gekkonid vertebrae are provided by Ganguly & Mitra (1958) and Werner (1961a). The cervical vertebrae, like all gecko vertebrae, are associated with small persistent intercentra that lie ventral to the intervertebral discs, or persistent notochord. In association

T a b l e 3. Attributes of the axial skeletons of carphodactyline geckos (data this study, sample size = 5 for all species, unless otherwise noted. For species for which PV = ? no skeletons were examined). PV = presacral vertebrae (modal); FC = rib-free cervicals; SR = sternal ribs (range); MS = mesosternal ribs (range); IR = inscriptional ribs (range, mode underlined); ME = mesosternal extention; RR = vertebrae bearing reduced ribs (abdominal vertebrae); LV = lumbar vertebrae; SV = sacral vertebrae; CV = caudal vertebrae (range); SP = autotomy septum-bearing vertebrae; AS = first caudal vertebra bearing autotomy septum; red = reduced number.

Taxon (N if not 5)	PV	FC	SR	MS	IR	ME	RR	LV	SV	CV	SP	AS
Bavayia cyclura	26	3	2	2	0	+	6	1	2	26	all	6
B. sauvagii	26	3	2	2	0	+	6	1	2	30	all	6
Carphodactylus laevis	26	2-3	2	3	3	—	3	2-3	2	47	1-2	5
Eurodactylodes symmetricus	26	3	2	2	6	—	5	1	2	35	all	6
E. vieillardi	26	3	2	2	6-7	—	6	1	2	31	all	6
Hoplodactylus chrysosireticus	?	?	?	?	?	?	?	?	?	?	all	?
H. duvaucelii	26	3	2-3	2-3	0-1	+	6	1	2	32	all	6
H. granulatus	25	3	2	2	2	—	5	1	2	31	all	6
H. maculatus	26	3	2	2	0-1	+	5	1	2	29	all	6
H. pacificus	26	3	2	2	0	+	4-5	1	2	29	all	6
H. rakiurae (1)	26	3	2	2	0	—	4	1	2	28	all	6
H. stephensi (3)	26	3	2	2	0-1	+	5	1	2	32	all	6
Naultinus elegans	27	3	2-3	2-3	2-4	—	5	1-2	2	33	red	6
N. gemmeus	25	3	2-3	2-3	2-3	—	4	1	2	32	red	6
N. grayii	27	3	3	2	3-4	—	4	1	2	36	red	6
N. manukanus	?	?	?	?	?	?	?	?	?	?	red	?
N. poecilochlorus	?	?	?	?	?	?	?	?	?	?	red	?
N. rudis (3)	26	2-3	2	3	2	—	5	1	2	30	red	6
N. stellatus (1)	27	3	2	3	2	—	4	2	2	30	red	6
N. tuberculatus	?	?	?	?	?	?	?	?	?	?	red	?
Nephrurus asper	26	3	3	2-3	1	—	3	2	2-3	23	none	—
N. deleani (3)	25	3	3	2	1	—	4	1	2-3	26	1-2	6
N. laevissimus	26	2-3	3	2-3	0-2	—	3	2	2-3	25	1-2	6-7
N. levis	26	3	3	2	1	—	3	2	2-3	27	1-2	6-7
N. milii	26	3	3	2	0-1	—	3	2	2	35	1-2	6
N. sphyrurus (4)	26	3	3	2-3	1	—	3	2-3	2	22	1-2	6
N. stellatus (2)	24-25	2-3	3	2	0-1	—	4	1	2-3	24	1-2	6
N. vertebralis	26	3	3	2	0	—	3	2	2	32	1-2	6
N. wheeleri	26	3	3	2	0-1	—	3	2	2-3	?	1-2	6
Phyllurus caudiannulatus	26	3	2-3	3	1-2	—	4	2	2	30	1-2	5
P. cornutus	25	3	2-3	2-3	3-4	—	4	2	2	30	1-2	6
P. platurus	25	3	3	2	1	—	3	2	2	31	1-2	6
P. salebrosus	25	3	3	2	2-4	—	3-4	1-2	2	27	1-2	6
Rhacodactylus auriculatus	26	3	3	2-3	2-3	—	4-5	1	2	28	all	6
R. australis	27	3	2	2	3-4	—	4	1	2	29	all	6
R. cavaticus	?	?	?	?	?	?	?	?	?	?	all	?
R. chahoua	26	3	3	2	1	—	5	1	2	31	all	5
R. ciliatus	26	3	2	2	0-1	—	6	1	2	30	all	5
R. leachianus	26	3	3	2	3-4	—	4	1	2	22	all	7
R. lindneri	26	3	3	2	0	—	4	1	2	28	all	6
R. sarasinorum (4)	26	3	3	2	1	—	5	1	?	?	all	6
R. trachyrhynchus	26	3	2-3	2	0-2	—	5	1	2	30	all	6

with the cervical vertebrae these intercentra are somewhat enlarged and form hypapophyses ventrally. Typically the cervical intercentra are relatively narrow; however, in *Rhacodactylus trachyrhynchus* (Hoffstetter & Gasc 1969) and perhaps other members of this genus, the intercentra are broad and bear posteriorly-directed hypapophyses.

Hoffstetter & Gasc (1969) listed formulae for the cervical vertebral series and suggested that some were primitive. This determination seems to have been based on the assumption that gekkonids tend to show the primitive condition. Their pattern "a" (three ribless vertebrae, three with short ribs and two with long, slender ribs) is widespread among the outgroups (Wellborn 1933) and appears to be plesiomorphic for carphodactylines. A reduced number of rib-free cervicals consisting solely of the atlas and axis is seen in some individuals of *Naultinus rudis, Nephrurus laevissimus, Nephrurus stellatus* and *Carphodactylus laevis* (see Tab. 3). Ribs attach to the vertebral centra at the parapophyses (synapophyses). In all carphodactylines the anterior cervical ribs are simple in structure, consisting of a short bony vertebro-costal element and occasionally a very small distal cartilaginous segment. The posterior cervical ribs bear elongate, somewhat posteriorly curving cartilaginous processes.

Trunk Vertebrae

Character 22: Neural spines of trunk vertebrae low, less than half of total vertebral height (0), or high, contributing to compressed appearance of animal (1).

The vertebrae of the trunk region consist of the sternal, mesosternal, interthoracolumbar and lumbar series (Kluge 1962). All of these designations are based on features of rib attachment rather than on vertebral morphology per se. Little variation in trunk vertebrae was noted among the taxa examined, however, *Carphodactylus* and *Eurydactylodes* have extremely high neural spines on all of the presacral vertebrae adding to the overall appearance of compression of the body (character 22). High neural spines occur only in a few species among the outgroup taxa and are interpreted as derived within the Carphodactylini.

Lumbar Vertebrae

Character 23: Two (or three) lumbar vertebrae present (0), or one lumbar vertebra present (1).

Lumbar vertebrae are defined as non-rib-bearing vertebrae immediately anterior to the sacrum. One to three lumbar vertebrae are typical for carphodactylines; two appear to be primitive for the tribe. This is the typical condition in the Diplodactylini, although a single lumbar vertebra is said to be the most common occurrence among gekkonines (Wellborn 1933). One lumbar is found in all species in New Caledonian carphodactylines, *Hoplodactylus, Rhacodactylus (Pseudothecadactylus)*, and in some *Naultinus, Nephrurus* and *Phyllurus*. Other members of these genera have two lumbar vertebrae. Three lumbar vertebrae were found in some specimens of *Carphodactylus laevis* and *Nephrurus sphyrurus* (character 23). This condition has been scored as a variant of the primitive state.

Romer (1956) stated that all fully limbed lizards have two sacral vertebrae. This is generally true of geckos, but three and even four sacral vertebrae occur in some carphodactylines. *Hemitheconyx* is also reported as having three sacral vertebrae (Wellborn 1933) as are certain other eublepharines (Kluge 1962). The condition results from the inclusion of the first pygal vertebra into the sacral complex (Holder 1960; Kluge 1962). The condition is variable among species of both *Nephrurus* and *Phyllurus* (Holder 1960).

Holder (1960; Moffat 1973a) regarded the loss of a sacral pleurapophyseal process in the Diplodactylinae as a putative synapomorphy. I have not located this structure in any carphodactyline. Moffat (1973a) stated that the process is present in all eublepharines and gekkonines. Kluge (1987) has indicated that it is present only in some diplodactylines and pygopodids. It thus seems unlikely that the reduction is a synapomorphy of the Diplodactylinae as a whole.

Caudal Vertebrae

Character 24: Pygal pleurapophyses decrease in size markedly distally A), or broadly expanded on all pygal vertebrae B).

Character 25: 30 or more caudal vertebrae (0), or fewer than 30 caudal vertebrae (1).

Character 26: Centra of caudal vertebrae elongate (0), or very short (sometimes shorter than wide) (1).

Character 27: Post-pygal pleurapophyses present (0), or absent or greatly reduced (1).

Character 28: Autotomy planes present in all post-pygal vertebrae (0), or absent in some or all post-pygal vertebrae (1).

Character 29: Autotomy planes absent from posterior half of tail A), or absent from all but one to three anterior vertebrae B).

Character 30: Anteriormost autotomy septum in sixth (or seventh) caudal vertebra A) (0), or in fifth caudal vertebra B) (1).

The anterior caudal vertebrae are generally similar in form to the posterior sacral but rapidly change shape posteriorly. Modified intercentra are present as haemapophyses (chevron bones) from about the third postsacral intervertebral region to almost the tip of the tail in most species. This appears to be the primitive condition for the group and is the norm in the outgroups (Wellborn 1933). The first haemapophysis may remain unfused throughout life in certain individuals. Holder (1960) reports fusion of anterior haemapophyses in some *Phyllurus* and *Nephrurus*. Like the centra, the smaller, more posterior haemapophyses may be somewhat irregular, and in those species with reduced tails the haemapophyses may be entirely lacking in the posterior-most quarter to half of the tail.

The caudal vertebrae may be divided into pygal and post-pygal series. The first post-pygal is reckoned as the anteriormost vertebra bearing an autotomy septum. The ability to autotomize the tail is primitive for the Carphodactylini and for the family as a whole. The septa of all carphodactylines corresponds to Etheridge's (1967) type 4 which lies posterior to the relatively short, posteriorly directed transverse process. The transverse

processes of the pygal series in the Eublepharinae, Gekkoninae and Diplodactylini generally decrease posteriorly and are substantially narrower than those of the posterior interthoracolumbar. This condition occurs in *Pseudothecadactylus* and all of the New Zealand and New Caledonian carphodactylines. The derived condition of extremely broad pygal transverse processes is found in all species of the remaining Australian genera (character 24). Caudal ribs (El-Toubi & Khalil 1950) are never present, although Stephenson & Stephenson (1956) reported them in unspecified New Zealand species.

The number of caudal vertebrae varies greatly among carphodactylines. The ancestral condition for lizards as a whole was probably high (50 or more) (Romer 1956), but it is difficult to assess the primitive condition for gekkotans, although this too was probably reasonably high. Wellborn (1933) cites approximately 40 caudals as the most common condition among Gekkonines although Werner (1965) found a range of 18-35 (mode 25) in Israeli geckos. As a whole, geckos have relatively short tails that account for roughly one half of the total length. Extremely short tails, however, are rare. Among the Diplodactylini they occur in the *Diplodactylus conspicilatus* and *D. elderi* groups. Postsacral vertebral counts do not always reflect tail length however; the knob-tailed gecko *Nephrurus vertebralis* has more than thirty caudals, more than many species with tails of "normal" length. I accept the number of approximately thirty as the primitive number of carphodactyline caudal vertebrae. Alternative derived states are seen in *Carphodactylus laevis* which averages 47 caudals and in several species with reduced counts — *Rhacodactylus leachianus* (22), *Nephrurus sphyrurus* (22) and some species of knob-tailed *Nephrurus* (see Tab. 3) (character 25). Werner (1961a, 1964) noted geographic and temperature related variation in vertebral number, but no intraspecific trends were noted in the species examined in this study.

All species of *Phyllurus, Nephrurus* and *Carphodactylus* possess greatly shortened caudal centra relative to the other carphodactyline genera and the outgroups (character 26). This is interpreted as a derived state within the tribe. In some specimens of *Nephrurus asper* even the anteriormost post-pygals (see below) may be shorter than wide. Fusions are frequent in the caudal vertebrae of this species and in large specimens, the entire tail may be ankylosed. All of these species except *N. sphyrurus* also exhibit the derived feature of reduced (usually absent) transverse processes on the post-pygal caudal vertebrae (character 27). Etheridge (1967) reported that a similar loss was independently derived in many lizard lineages. In general the processes occur on no more than two or three post-pygals. In *Nephrurus sphyrurus* the transverse processes are present for about half the length of the tail.

As discussed, autotomy is primitive for the tribe. Among the outgroups, autotomy is generally possible through any post-pygal vertebrae except the very smallest irregular posterior elements. In cases such as *Uroplatus* (Siebenrock 1893; Wellborn 1933) and *Stenodactylus* (Werner 1965, 1968) the site of autotomy is restricted to one or several planes. Among carphodactylines the primitive condition (all post-pygals autotomic) is found in most *Hoplodactylus*, all *Rhacodactylus (Pseudothecadactylus)* and all New Caledonian species. Site restriction to one or two vertebrae is typical of all species of the remaining Australian genera. *Nephrurus asper* is unique among gekkonids in lack-

ing autotomy septa entirely. A second derived condition is shared by all *Naultinus* and *Hoplodactylus granulatus*. This involves the restriction of autotomy to the first five to twelve post-pygal vertebrae (characters 28, 29). It is not clear that one condition is derived from the other; therefore each is regarded as a separately evolved apomorphy. It is noteworthy that, with the exception of *Nephrurus sphyrurus*, the feature of a reduced number of autotomy sites is coincident with the loss of transverse processes. The same phenomenon is also reported for *Uroplatus* (Siebenrock 1893; Wellborn 1933). Thus it appears that the lack of transverse processes may preclude autotomy although the reverse is generally, though not necessarily, so.

The site of the first autotomy plane also varies among members of the group. The first septum passing through the sixth caudal vertebra is the most common condition in the diplodactylines and probably for the gekkonines as well. Some intraspecific variation has been noted (Holder 1960), but I have found this to be minimal. I am in agreement with Holder on the presence of the rarer condition (first septum in fifth caudal vertebra) in *Carphodactylus laevis* but cannot confirm her report of a similar state in *Nephrurus milii*. Holder's (1960) variable states in *P. platurus* may in fact represent the inclusion of two taxa, *P. platurus* and *P. caudiannulatus*, in her sample. I have found that the former typically displays the more common condition while the latter invariably exhibits the rare condition. In this species pair the total number of pre-autotomic vertebrae is equal at 32. The former species, however, possesses one fewer presacral and one more pygal vertebra than the latter. Because it appears likely that both counts are the result of a single shift in sacral placement, only the derived state of the autotomy site shift in *P. caudiannulatus* was considered in the phylogenetic analysis. Werner (1965) reported a similar situation in specimens of *Tropiocolotes steudneri* in which a shift in the first autotomy site was accompanied by a complementary change in the number of presacral vertebrae. Among the non-Australian taxa, the more anterior first autotomy septa was also found in *Rhacodactylus chahoua* and *R. ciliatus* (character 30). A second apomorphic state is seen in *Rhacodactylus leachianus*, in which the seventh caudal vertebra always contains the first autotomy septum.

Ribs

Character 31: Mesosternal extension absent A)(0), or present B)(1).

Character 32: Inscriptional ribs generally absent or one A), two, three, or four B), or five, six, or seven C).

Character 33: Abdominal ribs five or six (modal number) A), or three or four (modal number) B).

The sternal ribs (Fig. 10) of carphodactylines, like all gekkonid ribs, are holocephalous and originate on the parapophyseal facet on the lateral face of the centrum. Thoracic ribs are generally divisible into three segments: a bony vertebro-costal element (always present), a cartilaginous intermediate element, and a sterno- (or mesosterno-) costal element.

Sternal ribs attach directly to the sternum. Mesosternal ribs connect to the sternum via a mesosternum or "xiphisternum" (Fig. 11). In carphodactylines this structure consists

of narrow, paired bands of cartilage running posterior from the sternum along the mid-ventral line of the body. It forms as the result of the fusion of the cartilaginous portions of the adjoining ribs. A small mesosternal extension may continue posteriorly from the junction of the mesosternum and posteriormost mesosternal rib. Sternal ribs and mesosternal ribs number between two and three in the carphodactylines and the number of either may vary within a single species (Tab. 3).

Bavayia (Fig. 10b) and some species of *Hoplodactylus* have mesosternal extensions (character 31). In contrast to Kluge's (1967b) observations, I saw only small extensions in these forms and none in *Naultinus, Carphodactylus* or *Nephrurus*.

Parathoracic ribs (Weber 1835; Hoffstetter & Gasc 1969) or inscriptional ribs (sensu Kluge 1967b) are those that lie caudad to the mesosternal ribs and curve anteriorly to approach the mesosternum along the midline. In many cases these paired elements fuse at the midline, forming a chevron. Free chevrons (parasternalia sensu Remane 1936) are absent in carphodactylines and in most geckos in general. *Uroplatus fimbriatus*, a gekkonine, is unique in its possession of 13 fused inscriptional ribs including three free parasternalia (Siebenrock 1893; Wellborn 1933). Among members of the tribe Carphodactylini, between zero and seven inscriptional ribs were recorded. The number frequently varies by one or (rarely) two within a species. It appears that the same rib in different animals may or may not fuse to the mesosternum. Thus, the sum of mesosternal and inscriptional ribs within a species is usually constant. Kluge (1967b) provides generic summaries of rib counts, but because this lumps species it is not particularly useful for my analysis.

Species of both *Nephrurus* and *Hoplodactylus* typically bore two to three inscriptional ribs. Three were recorded in *Carphodactylus* and zero to four were found in *Phyllurus* and *Rhacodactylus*. A minimum of six sets of inscriptional ribs, most fused, were found in both species of *Eurydactylodes* (Tab. 3) (character 32). Kluge (1967b) summarized inscriptional rib counts within the species groups of *Diplodactylus* and determined that an increased number of inscriptional ribs characterizes primarily arboreal taxa. This was hypothesized as being an adaptation to prevent visceral sagging and to increase the area for muscle attachment. A similar trend was seen when comparing the primarily arboreal species of carphodactylines with the terrestrial *Nephrurus*. Conflicting evidence from the successive outgroups prevented assessment of the polarity of this character.

"Abdominal" ribs lacking intermediate and mesosternal elements typically number four to six in the New Caledonian and New Zealand taxa as well as in *Rhacodactylus (Pseudothecadactylus)*. Three to four are found in the remaining Australian genera (character 33).
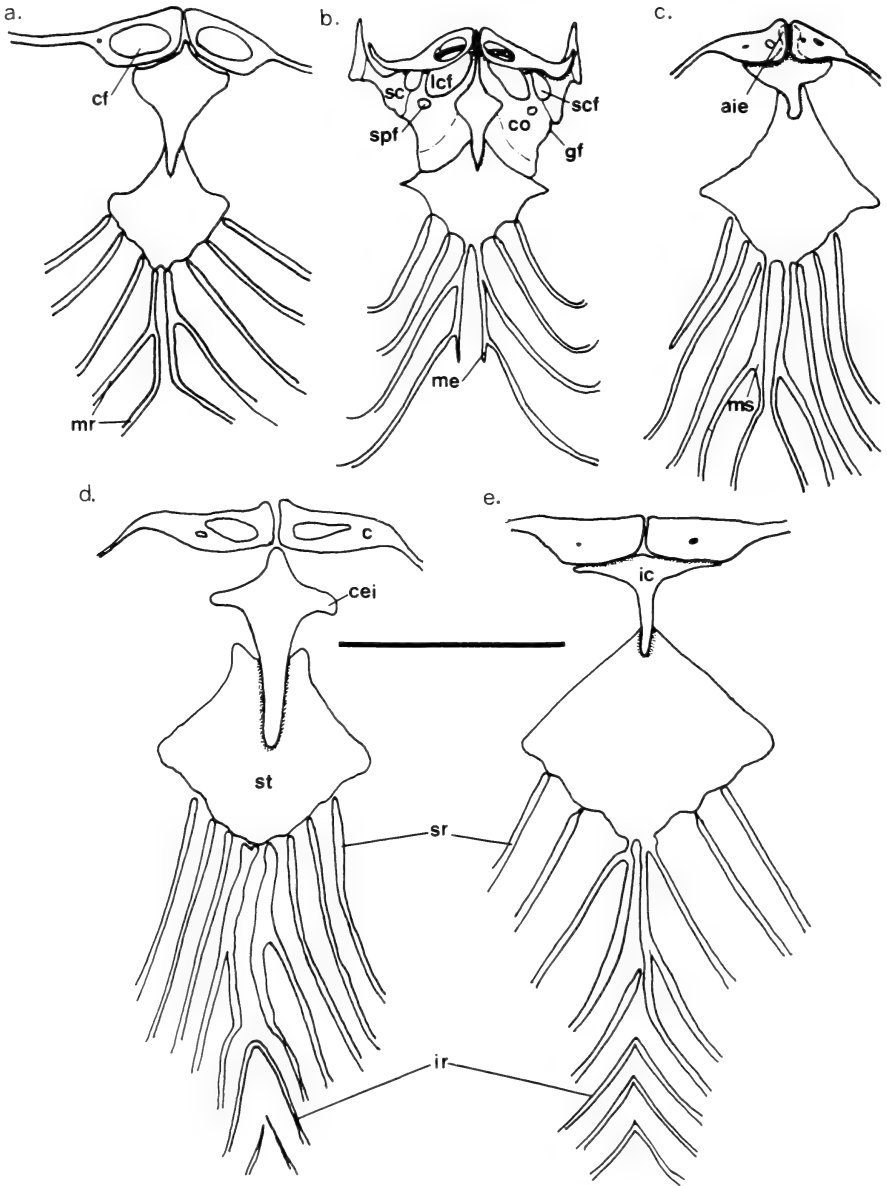
Fig.10: Sternum, pectoral girdle and ribs of selected carphodactyline geckos. (a) *Nephrurus levis* (AMS R20451), (b) *Bavayia sauvagii* (CAS 165905), (c) *Phyllurus platurus* (AMB, no number), (d) *Rhacodactylus auriculatus* (CAS 165895) and (e) *Phyllurus cornutus* (AMS R20477). Scapulo-coracoid shown in b only. Note the differences in mesosternum (character 31), ribs (character 32),

Sternum, Pectoral Girdle and Forelimb

Sternum

Character 34: Sternum long and broad (0), or short and narrow (1).

Character 35: Sternum ossified in adult (0), or cartilagionous (1).

The sternum in all carphodactylines is a rhomboidal plate straddling the ventral midline of the trunk. Primitively it is both broad and long relative to the interclavicle and medial portion of the clavicle. In all species of *Nephrurus*, especially *N. sphyrurus*, the sternum, although maintaining the same shape and position, is relatively much smaller than in other species (character 34) (Fig. 10). This condition does not occur in examined species of the outgroup taxa and is interpreted as being derived. Primitively in each of the successive outgroup taxa the sternum ossifies more or less completely through pre- and early post-natal ontogeny. As noted by Stephenson & Stephenson (1956), in *Naultinus* the sternum shows the apomorphic and paedomorphic condition of remaining unossified throughout post-natal ontogeny (character 35). No trace of an enclosed sternal fontanel (see Camp 1923) was found in any of the carphodactyline specimens examined. However, an emargination open posteriorly between the mesosternal rods (as reported by Kluge 1962, in *Coleonyx*) was found to occur in some *Phyllurus caudiannulatus* and *P. cornutus* (Fig. 10). This character was not scored because it was variable within these taxa and depends largely on the extent of mesosternal fusion.

Interclavicle

Character 36: Interclavicle imperforate (0), or perforate (1).

Character 37: Anterior process of interclavicle (if present) narrow and splint-like (0), or terminating in a broadened disk (1).

Character 38: Anterior process of interclavicle present (0), or absent (1).

Character 39: Coracoid processes of interclavicle anteriorly located A)(0), or located posteriorly along interclavicular body B)(1).

Character 40: Coracoid process of interclavicle distinctly narrowed and elongate (0), or broad and indistinct (1).

Character 41: Coracoid process of interclavicle does not contact clavicle (0), or does contact clavicle (1).

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sternum and interclavicle (characters 34, 36—41), clavicle (characters 42—43). Scale bar = 10 mm. Abbreviations are as follows:

aie — anterior interclavicular extension	me — mesosternal extension
cei — coracoid extension of interclavicle	mr — mesosternal ribs
cf — clavicular fenestra	ms — mesosternum
co — coracoid	sc — scapula
gf — glenoid fossa	scf — scapulocoracoid fenestra
ic — interclavicle	spf — supracoracoid foramen
ir — inscriptional ribs	sr — sternal ribs
lcf — lateral coracoid fenestra	st — sternum

Immediately anterior to the sternum, and also in the ventral midline, lies the interclavicle, a dermal bony element present in all geckos, although greatly reduced in the aberrant gekkonine *Uroplatus* (Siebenrock 1893). Even in highly circumscribed groups the shape of the interclavicle may vary widely (Noble 1921; Kluge 1967b). In the primitive condition within carphodactylines the interclavicle is considerably longer than wide and bears a pair of laterally directed coracoid extensions just posterior to the clavicles. Posteriorly the interclavicle inserts into a depression of the sternal apex. The cartilaginous epicoracoids support the interclavicle and bridge the gap between this element and the scapulocoracoid proper. A small anterior extension of the interclavicle sometimes runs deep to the clavicles. The interclavicle is primitively imperforate in the outgroups to the Carphodactylini. However, fenestrations sometimes occur in the widest part of the bone in *Carphodactylus* (Kluge 1967b) and *Nephrurus* (excluding *N. sphyrurus*) (character 36). This condition is interpreted as apomorphic. A unique broadened disk is present at the terminus of the anterior interclavicular extension in *Phyllurus caudiannulatus* and *P. platurus* (character 37). In the remaining two species of leaf-tails the anterior extension has been completely lost, yielding in a T-shaped interclavicle (character 38) (Fig. 10). In all other species the primitive condition of a narrow, tapering splint characterizes the anterior interclavicular process as it does in the outgroups.

In members of the outgroups, and primitively in the carphodactylines, the coracoid extensions of the interclavicle, which may project slightly anteriorly or posteriorly, are placed far anteriorly on the element, just posterior to the clavicles. Exceptions are seen in *Bavayia* and *Rhacodactylus (Pseudothecadactylus)* in which the extensions originate far posteriorly on the interclavicular body (character 39). As noted by Kluge (1967b), *Carphodactylus* and *Nephrurus* are characterized by the apomorphic condition of a greatly expanded interclavicle (character 40). In *N. asper* and *N. deleani* the anterolaterally projecting coracoid extensions remain as distinct, though short processes. In the remainder of these forms the interclavicle anterior to the sternal extention is broadly expanded, resembling a rhomboid, but variation is more or less continuous. In all species of *Naultinus* a reduction of the element is seen. Stephenson & Stephenson (1956) referred to the interclavicle in this taxon as a splint. However, I have found that this bone generally has at least weakly developed coracoid extensions. The small size and somewhat irregular shape of this element probably reflects its truncated development. It appears to form late in pre-natal ontogeny. The coracoid extensions of the interclavicle do not touch the clavicles except in *Carphodactylus, Nephrurus* and *Phyllurus* (Fig. 10) (the latter two variably within species) (character 41).

Clavicle

Character 42: Clavicular fenestrae present (0), or absent (rarely present as minute openings) (1).

Character 43: Clavicular fenestrae small to moderate in size A)(0), or very large B)(1).

Anterior to the interclavicle are the paired dermal clavicles, which meet at the midline deep to the anterior extension of the interclavicle (if present). For carphodactylines a

broadly expanded and fenestrated medial portion is primitive. The lateral portions of the clavicles extend dorsally along the curve of the coracoid border, terminating deep to the antero-ventral border of the suprascapula. As described for *Hemidactylus flaviviridis* (Mahendra 1950), there is a small depression in the suprascapula that receives this process. Stephenson & Stephenson (1956) reported the clavicles as imperforate in *Naultinus elegans*, although Kluge (1967b) found minute fenestrae in this species and large fenestrae in *"Heteropholis"*. I found generally small to minute fenestrae in *Naultinus*. Although there is generally one fenestra per clavicle, there may be as many as three, and fenestral number may be asymmetrical. Fenestral size varies widely in the group and is highly variable within genera (Kluge 1967b). Fenestrae are generally absent in *Carphodactylus* and *Phyllurus* (Stephenson 1960; Kluge 1967b) (character 42). Exceptionally large fenestrae may be present in *Nephrurus* (Fig. 10) (variable in *N. asper* and *N. wheeleri*) (character 43). Based on comparisons with outgroup taxa both the enlarged and reduced fenestral conditions are derived.

Scapula

Character 44: Scapula possesses a short, stout blade (0), or scapular blade elongate with narrow shaft (1).

The primary paired lateral components of the pectoral girdle are in the scapulo-coracoids. Each of these compound elements is highly complex and is oriented with the flat coracoid plate at approximately right angles to the dorsally projecting scapula. The suture between these elements is visible only in some *Naultinus elegans* (Stephenson & Stephenson 1956), perhaps another indication of the paedomorphic nature of this genus. The scapulo-coracoid fenestrae perforate the element in the region of the embryonic suture, just anterior to the glenoid fossa. A large lateral coracoid fenestra occurs just medial to this. Finally a supracoracoid foramen penetrates the plate posterior to the lateral coracoid fenestra and anteromedially to the glenoid. The foramen is always contained entirely within the coracoid. The fenestrae, however, in some individuals of most species are emarginate anteriorly and may be closed by a union with the epicoracoid cartilage (see Romer 1956 for a discussion of this term). Similarly the epicoracoids may form the medial border of the medial coracoid fenestra, represented by an emargination of the adjacent coracoid. In all species the epicoracoids overlap in the midline dorsal to the interclavicle.

The scapula is primitively broad dorsally at its border with the suprascapula, slightly narrower near its midpoint, and expanded again ventrally at the coracoid suture. All of the knob-tailed *Nephrurus* plus *N. sphyrurus* depart from this morphology and display an apomorphic condition of an elongate and narrow shafted scapula that flares rather abruptly both proximally and distally (character 44). In all species of carphodactylines the supracoracoids remain largely uncalcified and extend posteriorly in a broad plate.

The proximal elements of the forelimb (the humerus, ulna and radius) are largely invariant, except for size and proportion, among the carphodactyline genera. The individual elements are basically in agreement with descriptions of appendicular

osteology in other gekkonid taxa (Mahendra 1950; Wellborn 1933; Siebenrock 1893; Kluge 1962). A single brachial sesamoid, the patella ulnaris, is generally present in the tendon of the triceps in mature specimens of all species.

Generally the carpal series consists of a large proximal radiale and ulnare articulating with the epiphyses of the long bones. A small centrale is situated between these two elements and a pisiform of variable size articulates with the postaxial border of the distal epiphysis of the ulna. Distal carpals I—V are small, somewhat rounded elements basal to the metacarpals. This basic structure is maintained in many lineages and is primitive for the family as a whole (Kluge 1962; Mahendra 1950; Siebenrock 1893; Khalil & Sabri 1977a).

Metacarpals

Character 45: Metacarpal V shortest with I and IV subequal (0), or metacarpals IV and V subequal, shortest (1).

The metacarpals are splayed widely, V is the shortest. Metacarpals I and IV are next in size, and both are distinctly longer less robus V in the majority of carphodactylines. This condition is assessed as primitive on the basis of its distribution in the outgroups. In *Phyllurus* and *Carphodactylus*, however, metacarpals IV and V are similar in size and shape and both are distinctly shorter than metacarpal I (character 45). The structure of individual phalangeal elements is similar to that described below for the phalanges of the pes. Paraphalangeal elements are lacking in both the manus and pes of all carphodactylines.

Phalanges

Character 46: Phalangeal formulae 2-3-4-5-3 (manus) and 2-3-4-5-4 (pes) (0), or 2-3-4-4-3 (manus) and 2-3-4-4-4 (pes) (1), or 2-3-3-3-3 (manus and pes) (2).

The primitive phalangeal formulae for the Lacertilia are 2-3-4-5-3 (manus) and 2-3-4-5-4 (pes) (Romer 1956). The same formulae are plesiomorphic at the level of the Carphodactylini. Within the tribe variation is seen only among knob-tailed members of the genus *Nephrurus* (Stephenson 1960; Kluge 1967a). All species have been examined and found to conform to one of two patterns first delineated by Stephenson (1960). *Nephrurus asper* and *N. wheeleri*, the spiny knob-tails, show a single reduction in digit IV of the manus (2-3-4-4-3) and pes (2-3-4-4-4). The remaining five taxa show further reduction in digits III and IV of the manus and III, IV and V of the pes, yielding the formula 2-3-3-3-3 for both manus and pes (character 46). These two conditions are regarded as successive apomorphic states relative to an unreduced phalangeal complement. Among the Diplodactylini reduction occurs in *Diplodactylus stenodactylus* and *Rhynchoedura ornata* (manus only). Parellel reduction has taken place many times in other gekkonid lineages (Russell 1972, 1979a).

Pelvic Girdle and Hindlimb

The pelvic girdle is entirely endochrondral in origin. It consists of two tripartate innominate bones, each composed of a pubis, ischium and ilium. The pubis is the anteriormost element and lies ventrally in the body in a horizontal plane. Anteriorly the pubis contacts an epipubic cartilage in the midline. Near its posterior border it is pierced by the obturator foramen for the passage of the obturator nerve. It meets the other elements at the acetabulum, the receptacle for the femoral head. The sutures at the acetabulum are generally obscured although they are rarely visible early in postnatal ontogeny (Stephenson 1960) and in some adult *Naultinus* (Stephenson & Stephenson 1956).

The ischium runs as a horizontal plate postero-medially from the acetabulum to the ventral midline, where it contacts the medial ligamentum hypoischium and os hypoischium. The elongate ilium passes posterodorsally to lie just lateral to the sacrum. The space enclosed by the ventral portion of the innominate bones is the ischiopubic fenestra or cordiform foramen. In many lizards a medial ligament, which sometimes calcifies (Khalil & Sabri 1977b), bisects the ischiopubic fenestra (Mehnert 1891; Mahendra 1950). Such a structure has been reported in *Gonatodes, Sphaerodactylus* and *Aristelliger* (Noble 1921; Stephenson 1960), but may simply refer to an anterior extension of the hypoischium as reported in *Gonatodes* by Wellborn (1933). No medial ligament was observed in any of the carphodactyline geckos.

Epipubic Cartilage
Character 47: Epipubic cartilage small and wedge-shaped (0), or greatly expanded anteriorly to form a broad, thick pad (1).

The pubic bones of carphodactylines never directly contact one another at the pubic symphysis, but are separated by an epipubic cartilage. The primitive condition of a narrow, triangular epipubic cartilage with its apex directed posteriorly is shared by most carphodactylines, the Diplodactylini and most other geckos. In *Phyllurus cornutus* and *P. salebrosus*, however, the epipubis forms a greatly expanded wedge which may be as much as one half the size of a single pubic bone (Fig. 11) (character 47).

Pubis
Character 48: Pectineal process of pubis small and ventrally directed (0), or large and domed (1).

The primary plate of the pubis is relatively narrow, particularly anteriorly in most carphodactylines and their outgroups. In all species of *Phyllurus*, however, the pubis is broad and robust (Fig. 11). A pectineal tubercle or process is present anterior to the obturator foramen in all species. Curiously, Romer (1956) reported the structure absent in all geckos. However, it has been identified in all geckos examined to date (Noble 1921; Wellborn 1933; Stephenson 1960; Stephenson & Stephenson 1956; Kluge 1962; Mahendra 1950; Siebenrock 1893; Cogger 1964). The pectineal process is primitively weakly
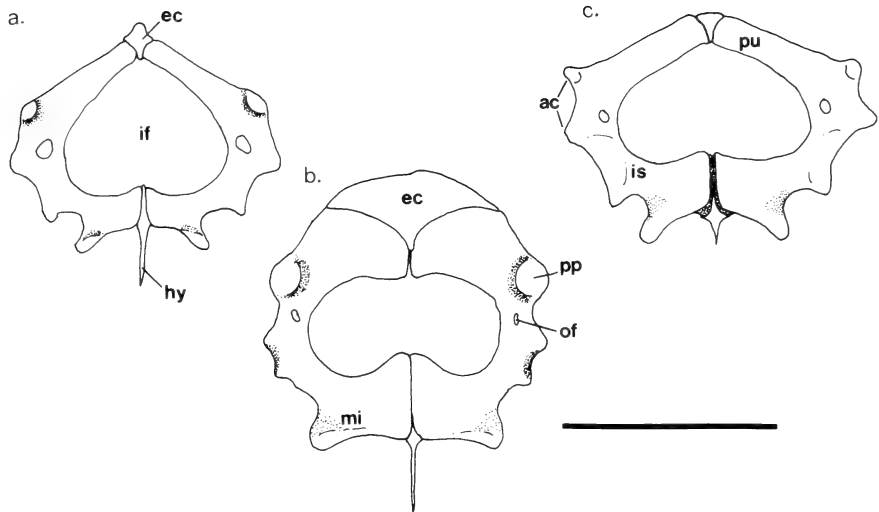
Fig.11: Ventral views of pelvis in (a) *Bavayia sauvagii* (CAS 165906), (b) *Phyllurus cornutus* (AMS R20447) and (c) *Naultinus elegans* (AMB 395). Note the differences in the size and shape of the epipubic cartilage (character 47), the pectineal processes of the pubis (character 48), the metischium (character 49) and the hypoischium (characters 50—51). Scale bar = 10 mm (b), 5 mm (a, c). Abbreviations are as follows:

ac — acetabulum	if — ischiopubic fenestra	of — obdurator foramen
ec — epipubic cartilage	is — ischium	pp — pectineal process
hy — hypoischium	mi — metischial process	pu — pubis

developed but projects ventrally in carphodactylines. A derived condition is seen in *Phyllurus*, in which the process is robust and domed (character 48).

Ischium

Character 49: Metischial processes narrowly separated from one another posteriorly (0), or expanded posterolaterally, widely separated from one another (1).

The posterior portion of the ischium bears a large, blade-like metischial process. The distance between the two metischial processes is generally small — less than the width of the ischiopubic fenestra in the Diplodactylini and the New Zealand and New Caledonian species of the carphodactylines (Fig. 11), as well as in *Rhacodactylus (Pseudothecadactylus)*. The remaining carphodactylines share the synapomorphy of a much broadened and expanded ischium and metischial process (character 49).

Hypoischium

Character 50: Hypoischium slender and narrow A), or short and dagger-shaped B).

Character 51: Hypoischium short (0), or extending posteriorly almost to level of vent (1).

A prominent hypoischium is present in all species (contra Arnold 1984, who reported this element as reduced or absent in *Hoplodactylus pacificus* and *Rhacodactylus trachyrhynchus* as well as in other diplodactylines and eublepharines). This feature was discussed by Camp (1923), who presented evidence against the hypothesis of Mehnert (1891), who believed that the hypoischium was an ancient portion of the ischial plate. Rather, the free hypoischium appears to be a continuation of the ligamentum hypoischium, which serves as the ischial symphyseal pad. Among eublepharines there appaers to be little posterior projection of the hypoischium (Kluge 1962; Khalil & Sabri 1977b) and in the Diplodactylini and many gekkonines the hypoischium is splint- or dagger-shaped and extends posteriorly a short distance posterior to the metischial process. Among carphodactylines the hypoischium is slender and elongate in *Carphodactylus, Phyllurus* and *Nephrurus*. A shorter, dagger-shaped process occurs in all of the New Zealand and New Caledonian forms as well as in *Pseudothecadactylus* (character 50). The polarity of these character states cannot be assessed by use of the outgroup method. The hypoischium is generally calcified, but is never so in *Naultinus*, in which the hypoischium resembles the diamond-shaped element figured in adult *Uroplatus fimbriatus* (Siebenrock 1893; Camp 1923). All of the knob-tailed *Nephrurus* share the apomorphic condition of an extremely elongate, slender hypoischium, extending posteriorly to the level of the medial cloacal bones (character 51).

No consistent variation was noted in the ilium. The overall shape of the ischiopubic fenestra varies greatly within the Carphodactylini. The Australian padless genera show a relatively smaller angle between the pubis and ischium, yielding a compressed oval foramen. In other genera the fenestra is more strictly cordiform. This is particularly so in *Naultinus*.

Little information of systematic value was obtained from the proximal elements of the hindlimb. The morphology of the femur, tibia and fibula is adequately described in other geckos (Mahendra 1950; Wellborn 1933; Siebenrock 1893; Kluge 1962). A patella tibialis is generally present on the preaxial face of the femoral-tibial joint in the tendon of the quadriceps group. A parafibula is rarely ossified. Lunulae are present as tiny sesamoid ossifications in the knee capsule of some particularly large specimens. These are most evident in the immense *Hoplodactylus delcourti* (Bauer & Russell 1986). Like all sesamoids, the presence of these bones is highly variable and is generally unreliable for systematic uses (Fürbringer 1900; Kluge 1962).

Metatarsals

Character 52: Metatarsals I and V shortest (0), or metatarsals IV and V shortest (1).

Character 53: Increasing order of metatarsal length V-I-IV-II-III A), or V-I-II-IV-III B).

Character 54: Metatarsal V slightly hooked A), or greatly hooked B).

Character 55: Digits of pes all splayed due to metatarsal position (0), or digit V almost opposable to I—IV (1).

Character 56: Metatarsals I—IV $\leq$ 150% length of longest phalanx (0), or approximately twice length of longest phalanx (1).

Character 57: Metatarsals III and IV diverging (0), or parallel (1).

The structure of the gekkonid tarsus, as well as that of the pes proper, has been considered by numerous authors (Russell 1972, 1975; Haacke 1976; Khalil & Sabri 1977a). Russell (1972) surveyed the majority of genera in the family and provided osteological information, especially for the metatarsals and pedal phalanges, for many carphodactyline species.

Primitively for the tribe, a basal tibiofibulare or fused astragalus and calcaneum but (see Broom 1921 for a different interpretation) articulates with both the tibia and the smaller fibula. As described by Kluge (1962) for *Coleonyx*, a large cuboid lies basal to metatarsal IV. Smaller distal tarsals are basal to metatarsals I and III, and sometimes II (Stephenson 1960). Metatarsal V also articulates with the tibiofibulare and the cuboid as well as with its associated proximal phalanx. Three patterns of metatarsal length (from shortest to longest) are seen among carphodactylines. The pattern V-I-IV-II-III characterizes *Nephrurus* and *Naultinus*; V-IV-I-II-III is typical for the leaf-tailed *Phyllurus* and for *Carphodactylus laevis*; V-I-II-IV-III is typical for the remaining species in the tribe. Among the outgroups metatarsals V and I are the shortest in the Diplodactylini and in Eublepharinae (the character is variable among gekkonines). On this basis the pattern involving metatarsals V and IV as the shorter elements are regarded as derived (character 52). However, no a priori polarity of the remaining two patterns is suggested.

Metatarsal V is generally hooked in lepidosaurs (Robinson 1975) and serves as a site of attachment for most of the crural musculature. In general the structure of this element permits the foot to grip the substrate and to serve as a heel-analogue (Vialleton 1924; Schaeffer 1941; Robinson 1975; Russell & Rewcastle 1979; Brinkman 1980). In all of the padded genera metatarsal V is strongly hooked, while in the padless Australian genera, there is only a slight hooking (character 54). The polarity of this character could not be assessed on the basis of outgroup comparison.

The placement of metatarsal V generally causes digit V to splay away from the remaining digits in geckos. This is further accentuated in the knob-tailed *Nephrurus*, in which the remaining four digits are tightly bound together by connective tissue to yield an almost opposable digit V (character 55). Further, all knob-tails except *N. asper* and *N. wheeleri* share the derived condition of having metatarsals I through IV approximately twice the length of the longest phalanx of their respective digits (character 56). A similar condition has been reported in the gekkonine *Rhoptropus afer* (Haacke 1976; Wellborn 1933).

In the outgroups and carphodactylines, metatarsals I—IV diverge distally. This pattern is typical in *Phyllurus* and *Carphodactylus* and in *Nephrurus milii* and *N. sphyrurus*, although in some specimens metatarsals I and II, or II and III may be more or less parallel to one another. All remaining members of the tribe show the derived condition of parallel metatarsals III and IV (character 57).

Phalanges

Character 58: Metatarsal-phalangeal joint and first interphalangeal joint with little or no inflection (0), or strongly kinked (1).

Many features of internal digital structure vary within the carphodactylines, but most appear to be coincident with other osteological or external features. Russell (1972) discussed the pes of several species in detail, including *Rhacodactylus auriculatus* and *Carphodactylus laevis*. In general, the internal features, which include the presence of subdigital adipose pads and blood sinuses, are characterized by Russell (1972) as morphological transition series within the padded carphodactylines, from *Heteropholis* through *Naultinus* to *Hoplodactylus*, the New Caledonian species and eventually to the most pedally complex group, *Pseudothecadactylus*.

The phalanges are generally relatively wide, depressed and crescentic distally in padded forms and stout and deep in padless forms. Slight kinks are present in the digits of all species as a result of angulation between the proximal phalangeal elements and the metatarsals. However, a prominent kink is a derived condition for *Phyllurus* (character 58). This is achieved by the strong angulation of the joints between the metatarsal and phalanx one and between the proximal two phalanges. Elsewhere among geckos, the condition is paralleled in members of the genus *Cyrtodactylus* (Russell 1972, 1976, 1979a).

A strongly arcuate and slender penultimate phalanx is typical of many pad-bearing geckos (Russell 1972, 1979a) but is not universal. The function of the arcuate phalanx was discussed by Russell (1975). This condition is derived relative to the short, generally straight penultimate phalanx found in the Diplodactylini, Eublepharinae and many gekkonines. Among carphodactylines, the apomorphic condition is seen in all species of pad-bearers, although it is only weakly developed in *Naultinus* and in some *Hoplodactylus*. It has not been scored separately because its distribution is identical to that of certain functionally coupled external features treated later.

Cloacal Bones

Character 59: Lateral pair of cloacal bones absent (0), or present (1).

One or two pairs of small bones are typically present in association with the pygal region of male gekkonids. The medial pair of bones is present in all diplodactylines. These are slender semi-lunate or "J"-shaped bones lying along the anterior margins of the cloacal sac apertures. The lateral bones, which are variably present, are generally flattened and irregularly shaped and lie along the ventro-lateral aspect of the tail base in association with the cloacal spurs. An additional ossification, a hemipenial bone has been found in at least some species of the aberrant gekkonine genus *Aristelliger* (Russell 1977b; Kluge 1982). Cloacal bones were first noted by Schlegel (1838) in *Gekko japonicus* and have since been reported in most species of non-sphaerodactyline geckos (Wellborn 1933; Brongersma 1934; Underwood 1954; Kluge 1967a, 1982; Russell 1977b; Bastinck 1986) as well as pygopodids (Kluge 1967a, 1974, 1982). Somewhat similar elements are also found in the Xantusiidae (Savage 1957; Rieppel 1976a) and in the "prolacertilians" *Tanystropheus longobardicus* (Wild 1973) and *Tanytrachelos ahynis* (Olsen 1979). Kluge (1982) has argued that these elements in non-gekkonids are not

homologous. This view has received support from the recent reassignment of the fossil taxa from the Lepidosauria to the Archosauromorpha (Gauthier 1984; Benton 1984, 1985). Thus Rieppel's (1976a) claim that cloacal bones are primitive among the Lacertilia is based solely upon the presumed overall primitiveness of the taxa exhibiting cloacal ossifications. The bones and their associated cloacal sacs thus appear to be gekkonid synapomorphies (Kluge 1967a, 1982).

While the presence of bones and sacs may be regarded as apomorphic for the Gekkonoidea as a whole, the polarity of the presence of one versus two pairs of bones is more equivocal. Within the Diplodactylini, the immediate sister group of the Carphodactylini, both conditions occur. *Rhynchoedura* and most *Diplodactylus* have both medial and lateral cloacal bones, but the remaining taxa have only the medial elements (Kluge 1967b). The character is again variable in the Gekkoninae (excluding the sphaerodactylines and several other groups that lack the bones). In the tertiary outgroup, the Eublepharinae, however, all taxa have both sets of bones (Kluge 1962, 1967a). Kluge (1967b) considered two sets of cloacal bones as the derived condition within *Diplodactylus* and within the Diplodactylinae as a whole.
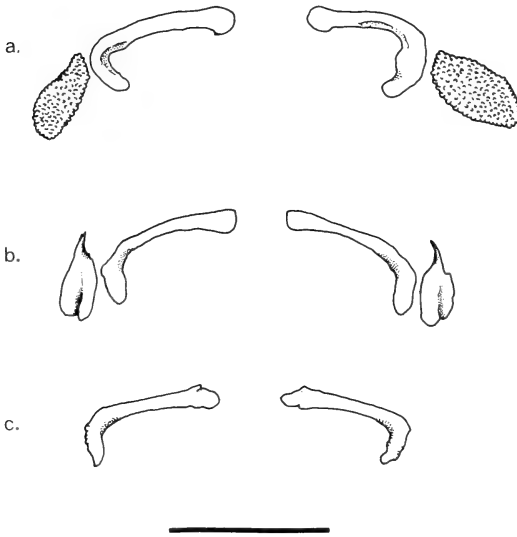
Fig.12: Cloacal bones in ventral view. (a) *Nephrurus milii* (NHMW 17424:1) — medial bones with lateral calcifications, (b) *Naultinus gemmeus* (MHNG 653.83) — lateral and medial bones present and (c) *Hoplodactylus maculatus* (MHNG 678.304) — medial bones only present. See character 59. Scale bar = 3 mm.

Both sets of bones are found in all species of *Naultinus* examined *(N. elegans, N. gemmeus, N. grayi, N. stellatus)* (Fig. 12b). Only the medial pair is present in the species of *Bavayia, Rhacodactylus, Eurydactylodes, Carphodactylus, Nephrurus, Phyllurus* and *Pseudothecadactylus*. Lateral calcium accretions were identified in two of seven adult male *Nephrurus milii* (Fig. 12a). These irregular accretions were found only in the largest specimens. I concur with Kluge (1967b) that these masses are not true cloacal bones. Members of the genus *Hoplodactylus* varied in this character, both among and

within species. Both pairs of bones were present in all *H. granulatus, H. rakiurae* and *H. stephensi* examined. The single known specimen of *H. delcourti* lacked the lateral bone as did 67% of *H. maculatus* (Fig. 12c), 33% of *H. pacificus*, and 25% of *H. duvaucelii. Hoplodactylus chrysosireticus* and *H. kahutarae* were not scored for this character (character 59).

Kluge (1967a, 1967b) considered the lateral cloacal bones to be highly variable in form and presence and recently postulated as many as six independent losses of the entire cloacal bone/sac system within the Gekkonoidea (Kluge 1982, 1987). The function of the system is still unclear but it appears that the medial bones are intimately related to the cloacal sacs (Smith 1933a) and perhaps to hemipenial stability (Wiedersheim 1876). The lateral bones have long been associated with the external cloacal spurs and the physical enlargement of the female's cloaca during copulation (Noble & Bradley 1933; Greenberg 1943; Russell 1977b).

Coloration

Character 60: Color pattern not primarily green (0), or color pattern predominantly green, fading to red or pink in preservative (1).

Character 61: Dorsal color pattern of head and nape unicolored or bearing a single band of color (0), or with three dark bards (1).

Character 62: Juvenile color pattern as adult or with dorso-lateral longitudinal markings A)(0), or with parvavertebral rows of light spots B)(1).

Green coloration is relatively rare among the Gekkonidae, in which it is primarily associated with diurnal forms. Among the sister-taxa to the Carphodactylini, this character state is lacking in all of the Diplodactylini and pygopodids. It occurs among certain gekkonines (sensu lato), most notably in *Phelsuma* (Schmidt 1912), certain *Lygodactylus*, and in numerous sphaerodactylines. Green coloration is absent in the Eublepharinae.

Among the carphodactylines, green coloration is seen in life among members of the genera *Naultinus, Hoplodactylus* and *Rhacodactylus*. A pale lime color is also present in some *Eurydactylodes vieillardi* and perhaps in *E. symmetricus*, and in some *Hoplodactylus rakiurae*. Olive green hues are sometimes seen in the background coloration of *H. maculatus, H. pacificus* and *H. chrysosireticus*. Yellow-green markings may also be present on some *H. granulatus*. Individuals of all species of the genus *Naultinus* may be primarily green, although male Banks Peninsula *N. gemmeus* and some *N. rudis* may be entirely brown and/or gray (Thomas 1982a; Robb 1980a) and some species, especially North Island forms, may be bluish or yellow instead of green. Among *Rhacodactylus* all *R. chahoua* and some *R. leachianus* exhibit green coloration. This is particularly striking in female *R. chahoua* (Bauer 1985a). No fresh specimens of *R. ciliatus* have been examined but Guichenot (1866) did not mention a green pattern in his color notes. Of the above mentioned taxa, only members of the genus *Naultinus* exhibit a fading to pink or violet (or occasionally blue or yellow) in preservative (Hut-

ton 1872; Fischer 1882; Robb & Hitchmough 1980). This fading has been observed in all species. In contrast, members of the other genera eventually fade to brown, gray or white. This difference in fading suggests that different mechanisms may produce the green coloration in life. Thus it seems prudent to regard the green coloration of *Naultinus* and *Rhacodactylus* as homoplastic. The fading condition found among the members of the genus *Naultinus* is here regarded as an apomorphic condition (character 60).

A unique barred pattern is characteristic of certain *Nephrurus* (character 61). Most specimens of *N. stellatus, N. laevissimus, N. levis* and *N. deleani* bear a pattern of three dark, dorsal bands across the head, nape and shoulders. This pattern is present, although obscured by the dorsal stripe, in *N. vertebralis. Nephrurus asper* and *N. wheeleri* frequently have dark markings on the nape and shoulders but usually in the form of a single broad band. The condition seen in the smooth knob-tails is regarded as derived.

Paravertebral stripes and spots are common in many species in the Carphodactylini, including specimens of most *Naultinus*, some *Hoplodactylus, Rhacodactylus auriculatus* and *Bavayia cyclura*. Variation within single taxa for this character was great, and at least in *Rhacodactylus auriculatus* individuals from the same locality varied from completely barred to completely striped. As a result this character was not used in the analysis. However, more stable taxon-specific patterns in juvenile coloring were noted and this character was used (character 62). Two character states were recognized: one in which juvenile pattern is simlar to that of the adult or in which markings are mid-dorsal, and one in which juvenile markings consisted of longitudinal rows of paravertebral light-colored spots. Most *Rhacodactylus* and *Hoplodactylus duvaucelii* showed the latter condition.

Membrane Pigmentation

Character 63: Tongue pinkish (unpigmented) (0), or distinctly pigmented (1).

Character 64: Mouth lining pinkish (unpigmented) (0), or distinctly pigmented (blue, black, yellow, or orange) (1).

Character 65: Parietal peritoneum unpigmented (0), or pigmented (1).

Character 66: Peritoneal pigmentaiton scattered (brown) A), or dense (jet black) B).

Besides variation in external coloration, several patterns of membrane pigmentation occur among carphodactylines. The first involve the coloration of the tongue (character 63) and the lining of the mouth (character 64). Based on outgroup comparison, the polarity of neither of these characters could be determined. Most geckos have pinkish or reddish mouths and tongues, reflecting a lack of pigmentation — the coloration being provided by the underlying blood vessels. Some gekkonines and many species of the genus *Diplodactylus*, however, have darkly pigmented mouths and tongues. Blue, black, yellow or orange tongues and/or mouths are present in at least some specimens of all species of *Naultinus*, in *Rhacodactylus australis* and in *Hoplodactylus*

granulatus, kahutarae and *stephensi* (see Appendix C for precise character state distribution). The primitive gekkonid unpigmented condition pertains in the case of the remaining carphodactyline taxa.

The absence of chromatophores in the lining of the parietal peritoneal membrane is taken to be plesiomorphic for carphodactylines and geckos as a whole and is probably associated with the primitive nocturnality of the Gekkota. The apomorphic condition of a darkly pigmented membrane is found in all *Hoplodactylus* and *Naultinus* examined (character 65). All Australian and New Caledonian species lack peritoneal pigmentation. In all *Naultinus* examined, and in *Hoplodactylus granulatus, H. rakiurae, H. kahutarae, H. duvaucelii* and *H. chrysosireticus* the peritoneum is jet black, while in the remaining *Hoplodactylus* there is a varying amount of scattered brown pigment (characters 66). Pigmentation of the bones (Greer 1967), meninges, and nervous and circulatory epithelia (Martinez Rica 1974) was not examined.

Eye

Pupil

Character 67: Pupil vertical with crenelated margins (0), or pupil vertical with smooth margins (1).

Pupil shape was the primary criterion used by Underwood (1954) in his division of the Gekkonidae into subfamilies. The usefulness of this character was subsequently questioned (Cogger 1964; Kluge 1964, 1967a) and the use of pupil shape in delineating relationships has since been generally abandoned. Kluge (1967a) argued that the condition of specimens (living, freshly killed, or preserved) influenced the apparent shape of the pupil and that within taxa there was considerable variation in pupil shape. Further, he identified and figured types intermediate between Underwood's straight vertical (diplodactyline) and "*Gekko*-type" pupil shapes. Other authors (Mann 1931; McCann 1955; Cogger 1964; Mertens 1972) have also discussed variation in pupil shape among geckos.

However, it appears that the character of pupil shape may indeed be useful. Greer (pers.comm.) has found, using uniform lighting on living specimens, that five major patterns of pupil shape may be identified. A crenelated margin, closing to a series of pin-holes ("*Gekko*-type"), occurs in most members of the Diplodactylinae and the Gekkoninae. A crenelate margin closing to four pin-holes is a gekkonine type pupil, while one closing to six-holes is characteristic of diplodactylines. Each subfamily, in turn, seems to demonstrate a peculiar pupil form among diurnal taxa. In the case of gekkonines, this is generally a circular pupil corresponding to Underwood's *Rhoptropus*-type. In the Diplodactylinae diurnal forms (i.e. *Naultinus*) exhibits a straight-edged, vertical pupil (character 67). All of the Diplodactylini possess the six-lobed pupil type and this is interpreted as primitive for the Carphodactylini. The derived pupil shape is shared by all *Naultinus*. This character needs to be verified in living *Hoplodactylus kahutarae* and in several of the South Island green geckos. However, I have had no trou-

ble identifying the pupil types in formalin fixed specimens and tentatively accept the results of examinations of preserved material.

Extra-brillar Fringe

Character 68: Extrabrillar fringe weakly developed (0), or larger, thick and prominent (1).

Non-eublepharine geckos share the derived condition of lidlessness and have a spectacle (Kluge 1967a). Within this monophyletic group, a lid-like extra-brillar fringe (Bellairs 1948) has evolved several times. The gekkonine *Ptenopus* has been identified as one form in which these structures are particularly highly developed and even moveable (Bellairs 1948; Kluge 1967a). These fringes, or folds, supposedly act to protect the eye and its spectacle from damage due to abrasion by wind-blown sand or soil encountered in burrowing (Bellairs 1948; Brain 1962; Kluge 1967a). They may also act as sun shield in those species that are partially active by day (Brain 1962).

Extra-brillar folds are well developed in all species of *Nephrurus* and in *Carphodactylus* (character 68). They are developed only weakly, or not at all, in the remaining carphodactyline taxa. Morphological information, as well as outgroup analysis, suggests that the extra-brillar folds are part of a transformation series including the simple brillar fringes present in many geckos (Smith 1935, 1939; Bellairs 1948). Among the lidless outgroups, prominent extra-brillar fringes are absent in the Diplodactylini and in pygopodids and occur only in phylogenetically scattered groups of gekkonines that are presumed to be derived with respect to this feature. An additional feature that is invariably coincident with the prominent fringes is the presence of a small patch of dark pigment on the inner lining of the extra-brillar fold. The function, if any, of this spot is unknown.

Ear

Character 69: External ear aperture small, oval (0), or large, vertically oriented (1).

Character 70: Aural opening free of skin folds (0), or partially occluded by flaps of loose skin (1).

Features of the inner ear have been used recently in a subfamilial level analysis of the Gekkonidae (Kluge 1987) and one character in particular, an "O"-shaped meatal closure muscle, appears to be a synapomorphy of the Diplodactylinae + Pygopodidae. Only external features of the ear were examined in the present study.

Among carphodactylines external ear size varies greatly. The auditory opening varies widely in size, but is generally oval in shape (the condition cannot be assessed in *Hoplodactylus delcourti* because this region of the specimen is distorted). This is similar to the condition seen in all examined species of the Diplodactylini, Eublepharinae and Gekkoninae. Members of the genera *Nephrurus, Phyllurus* and *Carphodactylus*, however, exhibit a generally vertically oriented ear opening, although

in *P. platurus* the opening may be only slightly higher than wide. This shape of the ear is interpreted as apomorphic (character 69).

Within the New Caledonian species of carphodactylines two additional derived aural features are seen. In all New Caledonian *Rhacodactylus* except *R. auriculatus* the ear is partially occluded by horizontal folds of skin, yielding a very narrow, slit-like aural opening (character 70). Within *Eurydactylodes* another feature, unique among geckos, is seen. Andersson (1908) first noted that a shallow groove runs from the angle of the mouth to the ear in *Eurydactylodes symmetricus*. The groove is lined with unscaled skin that merges imperceptibly with the oral epithelium. Its function is unknown. The condition is slightly different in *E. vieillardi*, in which a narrow band of skin interrupts the groove immediately anterior to the ear.

Endolymphatic System

The endolymphatic system of tetrapods consists of bilateral endolymphatic ducts which originate from the sacculus of the inner ear and may expand into endolymphatic sacs in the cranial vault after passing through endolymphatic foramina (Whiteside 1922). In certain iguanians, e.g. anolines, *Polychrus* (Etheridge 1959), *Cophotis ceylanica* and *Brookesia* (Moody 1983) and many geckos (Wiedersheim 1876; Kluge 1967a), the endolymphatic sacs are expanded extra-cranially and lie along the surface of the dorsal neck musculature. Frequently the sacs are filled with a calcium carbonate solution (Ruth 1918). This material, which generally solidifies in preserved specimens, has been identified as aragonite (Camp 1923; Kluge 1987).

The presence of enlarged endolymphatic sacs and "calcium-milk" has been interpreted as a synapomorphy of the Gekkoninae plus Sphaerodactylinae (Kluge 1967a, 1987). The plesiomorphic condition was believed to have been shared by all eublepharines, diplodactylines and pygopodids. Radiographs of preserved specimens show, however, that aragonite accretions are present in sacs in the nuchal region of both species of the New Caledonian genus *Eurydactylodes* (Bauer 1989b). Such sacs were not located in any other diplodactylines, nor in members of the Eublepharinae or Pygopodidae. The presence of these sacs is an independently derived synapomorphy of the species of *Eurydactylodes*. Bauer (1989b) reviewed hypotheses of endolymphatic calcium function and concluded that it is related to calcium stress in reproductive females. This feature is autapomorphic for *Eurydactylodes* and has not been included in the character analysis.

External Digital Characters

Character 71: Ventral digital scalation lamellate (0), or spinose (1).

Character 72: Digital lamellae without scansorial setae (0), or with scansorial setae (1).

Character 73: Scansorial pad narrow (0), or broadly dilated (1).

Character 74: Scansorial plates single (0), or divided (1).

Character 75: Apical plates of digit I single, medial A) (1); or cleft, asymmetrical with larger medial portion B) (0).

Lamellae, the rectangular subdigital scales present in many lizard groups, are universally present in eublepharines. They are present in most gekkonines and Diplodactylini except certain species of burrowing or sand-dwelling geckos including representatives of the genera *Chondrodactylus* (Haacke 1976) and *Stenodactylus* (Arnold 1980). Within the Carphodactylini the knob-tailed *Nephrurus* share the derived condition of a non-lamellate subdigital surface (character 71). In these forms the surface of the toes is spinose (Fig. 13a). The frequent association of this type of subdigital scalation with phalangeal reduction deserves further investigation.

Underwood (1954) stated that the Eublepharinae primitively lacked subdigital pads but did not provide explicit evidence for this belief. Russell (1972, 1976, 1979a) outlined the morphological features associated with primitive padlessness. His arguments are based primarily upon the absence of features permitting hyperextension — an ability necessary for the operation of the gekkonid scansorial apparatus. Among these features are the extensive overlapping of the dorsal and ventral regions of the interphalangeal

a   b   c   d   e   f   g
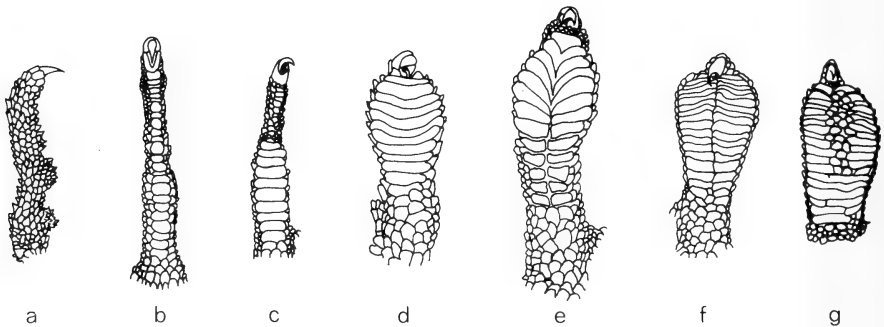
Fig.13: Toes of carphodactyline geckos. (a) Lateral view of digit I, right pes of *Nephrurus asper* (BMNH 1926.2.25.20) note spinose ventral scales (character 71). (b—g) ventral views: (b) *Phyllurus cornutus* (MNHN 1963.593) digit IV, left pes, (c) *Hoplodactylus granulatus* (BMNH 1946.8.22.71), digit IV, right pes, (d) *Eurydactylodes vieillardi* (BMNH (1926.9.17.7), digit II, right pes, (e) *Bavayia sauvagii* (BMNH 1926.9.17.25), digit IV, left pes, (f) *Pseudothecadactylus australis* (BMNH 77.3.3.12), digit IV, left pes and (g) *Rhacodactylus trachyrhynchus* (ZFMK 31809), digit IV, right pes (Figures a—f after Russell 1972). Note the differences in scansorial pad width and in scansor division (characters 72—74). *Rhacodactylus trachyrhynchus* possesses a unique lamellar pattern in which the scansors are fragmented medially (g).

joints and a relatively "simple" flexor musculature and tendonous system. Modifications of the digital units associated with hyperextension are present even in secondarily padless geckos (Russell 1976, 1979a) and determination of the primary padless condition is unambiguous. Using the outgroup comparison to assess polarity would result in determination of the padded condition as primitive for the Carphodactylini. However, examination of the digital structure reveals that the padless carphodactylines *Nephrurus, Phyllurus* and *Carphodactylus* (Fig. 13) are primitively so. This evidence is considered sufficient to establish the polarity of the character and the presence of pads in the Carphodactylini is interpreted as apomorphic (character 72). Secondary padlessness does not occur in any carphodactyline genera. Scansorial pads, when present, may be either narrow or broadly dilated. Again, based on Russell's (1972) arguments for a transformation series in digital structure, I accept as plesiomorphic the narrow condition, with the simpler musculo-tendonous structure. This condition pertains in all members of the genus *Naultinus* and in *Hoplodactylus granulatus, H. kahutarae* and *H. rakiurae*. The derived condition is seen in *Rhacodactylus (Pseudothecadactylus)*, the New Caledonian taxa and the remaining *Hoplodactylus* (character 73).

This determination of polarity for the presence of scansorial lamellae raises the question of the origin of pads. If we accept the preceding argument, then either all of the Diplodactylini are more closely related to some carphodactylines (i.e. to the padded species) than they are to others, or the padded conditions seen in the Carphodactylini and Diplodactylini (and the Gekkoninae) are independently derived. I believe the latter to be the case as presented in the "Introduction". Russell (1979a) discussed the spinose Oberhäutchen layer of the epidermis as a "universal primitive feature" from which the parallel, or shared but non-homologous, subdigital pads of the Gekkoninae and Diplodactylinae were derived. Yet he did not extend this concept to his analysis of pad evolution within the Diplodactylinae. I agree with Russell's (1979a) assessment that the Diplodactylini primitively bore terminal pads, yet there is little evidence to suggest that these share a common ancestry with the basal pads borne by the padded carphodactylines.

The acceptance of this hypothesis has some important ramifications for the polarity of other digital characters because homologies of character states cannot be inferred between the outgroups and the ingroup.

In those species with scansors, the pads may be either single or divided (character 74). Among the Carphodactylini the former condition pertains in all cases except *Bavayia* (Fig. 13e) and *Rhacodactylus (Pseudothecadactylus*, Fig. 13f) (Russell 1972, 1979a, considered *Bavayia* to possess truly divided scansors while those of the latter genus, except for the distalmost, were merely hinged as in *Hemidactylus*). Divided scansors have been considered as responses to functional demands and, as such, not valuable for assessing relationships (Vanzolini 1968; Russell 1979a). This position is clearly untenable, as the functional demand also has a history and reflects phylogeny at some level. Divided scansors function to maintain intimate surface contact when the penultimate phalanx becomes so arcuate as to lose its effective association with the

underlying blood sinus (Russell 1975). In these instances a separate branch of the sinus supplies each of the scansor rows (Dellit 1934; Russell 1976). In many specimens of typically single-scansored geckos, proximal scansors may be somewhat irregular and divided. A unique, regular division of the scansors, however, is seen only in *Rhacodactylus trachyrhynchus* (Fig. 13g). The functional significance of these median divisions of the scansors is unknown.
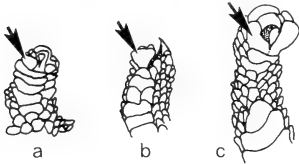

Fig.14: Terminal scansor (arrows) morphology of digit I in (a) *Eurydactylodes vieillardi* (BMNH 1926.9.17.7), right pes (completely divided terminal scansor), (b) *Bavayia sauvagii* (BMNH 1926.9.17.25), left pes (single scansor offset medially) and (c) *Hoplodactylus duvaucelii* (BMNH 54.11.6.4), left pes (single scansor, partially divided). See character 75.

Terminal scansors are present in the East Tasman genera of the Carphodactylini (Fig. 14). These structures do not resemble the apical plates of the Diplodactylini and are not considered strictly homologous to them. These are typically restricted to digit I of the manus and pes, and are absent in *Rhacodactylus (Pseudothecadactylus)*, which has lost the claw on these digits (see below). *Hoplodactylus rakiurae*, however, lacks this terminal scansor and *H. kahutarae* possesses scansors around the claws of all digits. The terminal plates are variously developed in the constituent taxa with the narrow-padded *Hoplodactylus* and *Naultinus* bearing smaller plates than the new Caledonian genera. *Eurydactylodes* may be distinguished from all other genera by its autapomorphic possession of two terminal plates, completely divided, on either side of the claw (Fig. 14a). All other species show either a single, medial scansorial plate or a single cleft plate, assymmetrical, with a large medial portion (character 75). The former condition is seen in all *Rhacodactylus* and in *Bavayia sauvagii* and *B. ornata* (Fig. 14b), the latter in *B. cyclura, B. crassicollis, B. montana, B. septuiclavis, B. validiclavis* and in the New Zealand species (Fig. 14c). The polarity of these character states could not be assessed and were entered into the analysis as missing for the ancestor.

Claws

Character 76: Claws present on all digits (0), or digit I clawless (1).

Character 77: Claws deep at base, moderately to strongly decurved (0), or slender at base, straight or only slightly decurved (1).

All carphodactyline geckos have claws on all digits with the exception of the species of *Rhacodactylus (Pseudothecadactylus)*, which lack claws (but retain the ultimate phalanx) on digit I of both manus and pes (character 76). In general, claws are high at the base, compressed, robust, and distinctly decurved. All Diplodactylini except the monotypic *Crenadactylus* (which is completely clawless) bear a total of 20 claws. This is the most widespread condition and would also appear to be plesiomorphic for the Gekkoninae (Bastinck 1981) as well as the Diplodactylinae.

The plesiomorphic claw shape occurs in most carphodactyline taxa, including *Pseudothecadactylus*. In all knob-tailed geckos of the genus *Nephrurus*, however, the claws are slender and narrow at their bases, and the curve of the claw, is slight (character 77). This unique morphology may relate to the completely terrestrial habits of *Nephrurus*, which would not require the robust, strongly decurved claws of those forms that are primary or occasional climbers. Invariably associated with the slender claws of *Nephrurus* are keeled periungulate scales, which may also be related to terrestrial locomotion.

Scalation Characters

Character 78: Dorsal body scalation heterogeneous A)(0), or homogeneous B)(1).

Character 79: Nostril contacts rostral scale A), or excluded from rostral scale B).

Character 80: First infralabials do not contact behind mental scale A)(0), or do contact behind mental scale B)(1).

Character 81: Postmental scales enlarged anteriorly A)(0), or subequal B)(1).

Character 82: Dorsal body scales without rosettes of surrounding scales (0), or tubercular with surrounding rosettes (1).

Character 83: Scales of rosettes not spinose A), or spinose B).

Character 84: Palmar scales only slightly smaller than scales on lower limbs (0), or sharply reduced in size relative to limb scales (1).

Character 85: Labial scales much larger than neighboring A)(0), or only slightly larger than neighboring scales B)(1).

Character 86: Infralabial scales broader than deep (0), or deeper than broad (1).

Character 87: Anterior loreal scales only slightly smaller than posterior loreals (0), or minute (1).

Many scalation features vary among carphodactyline species; few with any obvious functional correlates. For most such characters polarity cannot be reliably assessed by the outgroup method, so most were entered as unpolarized in the phylogenetic analysis. Those characters for which polarities could not be determined included: heterogeneous vs. homogeneous dorsal trunk scalation (character 78), rostral scale contacting or excluded from nostril (character 79), first infralabials contacting or not behind mental scale (character 80), and postmental scales enlarged anteriorly vs. uniform in size (character 81). These particular scale characters tended to show little relationship to presumed generic-level groupings, but were associated with lower level groupings of taxa (see Appendix C for the distribution of the states of these characters).

Atuberculate or simple tuberculate dorsal scales represent the primitive condition in the Carphodactylinae relative to the rosette-surrounded tubercles found in the species of the *Nephrurus* and *Phyllurus* (character 82). The rosette scales in turn may be either granular or spinose (character 83) but the polarity of this character could not be assessed. Another character that could be assessed was the size of the palmar scales. In the

primitive condition, the scales of the palmar surfaces are the same size or only slightly smaller than those of the wrist and post-axial forearm. Much smaller palmar scales characterize *Nephrurus milii* and *N. sphyrurus* (character 84).

Among the head scales, the labials may be much deeper than the surrounding scales (most carphodactylines) or they may be only slightly larger than their neighbors (character 85). The latter condition is found in the knob-tailed *Nephrurus*. Although the former condition is the most generally common among geckos, the latter is prevalent in certain of the Diplodactylini and the character polarity is ambiguous. Within the more common condition a further refinement in character state is possible. Some taxa, notably *Rhacodactylus* and *Eurydactylodes*, display the derived condition of the infralabials being deeper than broad (character 86). This is particularly notable in *Rhacodactylus trachyrhynchus*, in which all of the labial scales are extremely elongate.

Loreal scales are those relatively unspecialized scales occupying the region above the labials and between the eye and the nostril. In most geckos the anterior loreals are slightly smaller to slightly larger than the posterior loreals. This condition appears to be primitive for each of the outgroups and is interpreted as being plesiomorphic at the first outgroup node. Minute anterior loreals (character 87) occur in *Carphodactylus laevis, Nephrurus asper, N. levis* and *N. milii*, in which they are interpreted as a derived state.

Skin Folds and Webs

Character 88: Webbing absent between digits II, III, and IV (0), or webbing present between digits II, III, and IV (1).

Character 89: Webbing absent between digits IV and V (0), or webbing present between digits IV and V (1).

Character 90: No loose skin on posterior face of hindlimb (0), or folds of loose skin present on posterior face of hindlimb (1).

Character 91: Folds of loose skin around mandibular margins absent (0), or present (1).

Digital webbing is dependent on the presence of subdigital pads. Webbing between digits II and III and II and IV (character 88) is considered derived for carphodactylines and is found in the Tasmantis genera exclusive of *Naultinus*. Webbing between digits IV and V is less common (character 89) and is found only in *Rhacodactylus chahoua, R. ciliatus* and *R. leachianus*.

Body webbing or folds also occurs in some of the padded carphodactylines. Ventrolateral folds are common in most species of carphodactylines and in many other geckos. This may involve large margins around the body as in *Ptychozoon* (Russell 1979b), but more typically consists only of a slightly loose area between the axilla and groin. The fold is generally lined with adipose tissue and its size is, to some extent, a measure of the nutritional state of the animal. Besides these folds, which are considered plesiomorphic, certain carphodactylines possess loose folds of skin on the posterior

face of the hindlimb (character 90), frequently forming a mite pocket (Smith 1933a). This feature is shared by the species of *Eurydactylodes* and by *Rhacodactylus auriculatus, R. chahoua, R. ciliatus* and *R. leachianus*. The function of mite pockets has been considered by Arnold (1986). Loose skin folds along the margins of the mandible are further restricted (character 91) to *R. chahoua* and *R. leachianus*.

Preanal Organs

Character 92: Preanal organs present (0), or absent (1).

Character 93: Preanal organs extend onto thighs A)(0), or limited to preanal region only B)(1).

Two major epidermal gland types, generation glands and preanal organs, are found among the Gekkonidae (Maderson & Chiu 1970; Maderson 1972; Kluge 1983b). Among carphodactylines both preanal organs and beta-type generation glands occur (Bons & Pasteur 1977). Both are involved in holocrine secretion but the former is independent of the generation patterns of the remainder of the epidermis (Maderson 1970; Maderson & Chiu 1970). The function of both gland types is problematic (Cole 1966; Maderson 1985) but a role in reproduction (Greenberg 1943; Chiu & Maderson 1975; Menchel & Maderson 1975; Forbes 1941) or pheromone production (Maderson & Chiu 1984) has been implied.

Maderson (1970; Maderson & Chiu 1970) has considered the gland types as a transformation series with the following polarity: generation gland → preanal organ. Kluge (1983b) has correctly argued that this polarity, based upon current knowledge of gland distribution in lizards as a whole, should be reversed. Indeed, the ubiquity of preanal glands among lizards has long been recognized (Schaefer 1902).

Preanal organs are present in males of all carphodactylines except *Pseudothecadactylus cavaticus* (Cogger 1975a), all species of *Nephrurus* and most *Phyllurus*. Maderson & Chiu's (1970) reference to preanal organs in *P. cornutus* was not confirmed. However, male *P. salebrosus* do have small to moderate sized preanal organs and the specimens upon which Maderson & Chiu's comments were based may have been representatives of this species, which was undescribed at the time. Rösler (1985) also identified pores in *P. cornutus*, but again, the specimens may have been *P. salebrosus*. Preanal organs are present but reduced in size in *Carphodactylus* and *Rhacodactylus lindneri*. Pore patches are generally uninterrupted but may have a median gap of one to several scales in some species (e.g. some *Bavayia*, see Roux 1913). Absence of preanal organs is interpreted as a derived condition within the Carphodactylini (character 92).

Kluge (1967a, 1967b) used the character of a large median patch of preanal pores (Fig. 1) as diagnostic for the Carphodactylini. This condition is uniquely derived among geckos and is accepted as a synapomorphy of the tribe as a whole. Within the group, reduction to a single row of pores occurs only in members of the *Bavayia sauvagii* complex. All preanal pore-bearing species have pores in the trunk region just anterior to the cloaca. Extension of pore rows onto the thighs (= femoral pores) occurs in most

species but not in *Hoplodactylus pacificus, H. kahutarae, Rhacodactylus auriculatus, R. trachyrhynchus*, or in either species of the pore-bearing Australian *Rhacodactylus* (character 93). In several other New Caledonian taxa a somewhat intermediate condition (scored as "pores extend onto thighs") may occur. The polarity of this character could not be assessed.

Cloacal spurs

Character 94: Cloacal spurs few, flattened against tail base (0), or consisting of a cluster of six or more dorsolaterally directed scales (1)

Character 95: Scales of flattened cloacal spurs rounded, one to five in number A) (1), or pointed, two or more in number B) (0).

The cloacal spurs are sets of scales located at the postero-lateral margin of the vent, often associated with the lateral cloacal bones (if present). The spurs are frequently found in both sexes, but are particularly prominent in adult males. Three basic morphologies are represented among the Carphodactylini. In all species of *Nephrurus,*
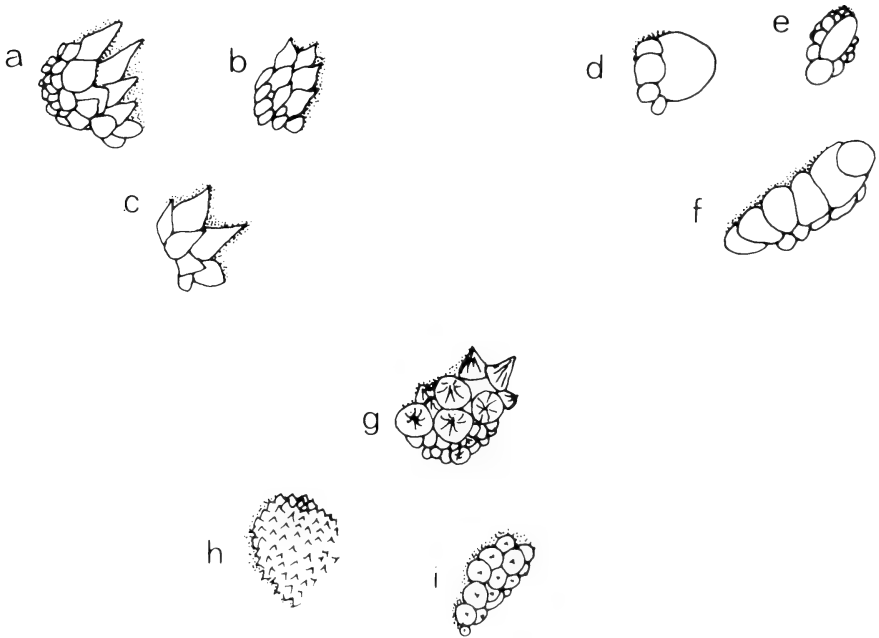

Fig.15: Cloacal spurs (characters 94—95). (a) *Naultinus stellatus*, (b) *Hoplodactylus stephensi*, (c) *Naultinus grayii*, (d) *Rhacodactylus lindneri*, (e) *Bavayia sauvagii*, (f) *Rhacodactylus chahoua*, (g) *Nephrurus wheeleri*, (h) *Nephrurus levis*, (i) *Phyllurus platurus* (a—c are left spurs — anterior to left; d—i are right spurs — anterior to right).

Phyllurus and in *Carphodactylus laevis* the entire spur cluster is inflated and directed dorsolaterally (Fig. 15g—i). The clusters consist of an oblong *(P. platurus, C. laevis)* to rounded (all other species) unit of six or more enlarged scales, usually conical and tuberculate. *Rhacodactylus, Eurydactylodes, Bavayia, Hoplodactylus duvaucelii, H. delcourti, H. maculatus, H. pacificus* and *H. chrysosireticus* (Robb 1980b) exhibit a second type of spur consisting of a single row of one to five enlarged, smooth tubercles that lie flat against the tail base and project posterodorsally (Fig. 15d—f). *Hoplodactylus stephensi, H. granulatus, H. rakiurae, N. grayii, N. stellatus, N. elegans* and *N. poecilochloris* (Robb 1980b) present a third pattern with a series of two or more flattened, pointed scales lying more or less flat against the tail base and projecting posterodorsally (Fig. 15a—c) (characters 94, 95).

The last two conditions are present in members of the Diplodactylini and superficially similar situations are seen among the members of the subsequent outgroups. It is not possible to determine the polarity of these two character states using outgroup comparison but the first condition described is unique among geckos and is apomorphic relative to other cloacal spur morphologies. *Carphodactylus* is further distinguished by a unique patch of dark pigmentation on the proximal portion of the spur.

Tail

Character 96: Tail elongate, tapering (0), or short, pyramidal (1).

Character 97: Tail with smooth margins (0), or leaf-shaped with ragged, flattened margins (1).

Character 98: Regenerated tail similar in shape to original (0), or short and bulbous (1).

Character 99: Cartilaginous rod of regenerated tail present, cylindrical (0), or absent or amorphous (1).

Character 100: Tail terminates in a conical point (0), or in a small knob (1).

Character 101: Dorsal scales of tail granular or tubercular A), or spinose B).

Character 102: Pygal region of tail tapers into post-pygal region (0), or abruptly decreases in diameter at pygal/post-pygal boundary (1).

Character 103: Scale rows on original tails at level of autotomy septa undifferentiated (0), or slightly smaller than neighboring rows (1).

Character 104: Ventral tail sulcus absent (0), or present (1).

Character 105: Subcaudal lamellae absent (0), or present (1).

Immediately posterior to the vent lies the pygal or pre-autotomic portion of the tail. Typically, ventral scales of this region are similar to those of the trunk venter, or only slightly larger. An autapomorphic condition seen in *Rhacodactylus australis* is the presence of enlarged hexagonal to octagonal scales in the subpygal region. This condition is evident in all specimens but is most pronounced in adult males.

Kluge (1967a) remarked on the extreme variability seen in gecko tails. Tail morphology seems to have been a primary component in the adaptive radiations of a number of gek-

konid groups (Russell & Rosenberg 1981; Vitt & Ballinger 1982). Several researchers have used characters of the tail in taxonomic studies of diplodactylines (Storr 1963; Covacevich 1975; Russell & Rosenberg 1981).

Tail shape in geckos, in general, may be described as elongate and cylindrical or subcylindrical. This form is characteristic of all of the Diplodactylini and most of the Eublepharinae and Gekkoninae. Among the Carphodactylini a highly modified form is seen in a number of groups. *Carphodactylus laevis* differs from all other geckos in its autapomorphic possession of a compressed tail. The remaining Australian padless species have another derived condition, a relatively short, pyramidal tail shape (character 96). In *Phyllurus* the tail ranges from unmodified (some *P. caudiannulatus*) to extremely broad and leaf-shaped. Leaf-shaped tails, typified by a thin fringed margin of skin, occur elsewhere among geckos only in the Madagascan *Uroplatus* and to some extent in species of *Ptychozoon*. This condition is considered derived for *Phyllurus* (character 97). Covacevich (1975) stated that the regenerated tail of *P. caudiannulatus* is always cylindrical. However, a number of specimens with typical, leaf-shaped regenerates were examined in this study.

In the knob-tailed *Nephrurus* the tail is always moderately broad and short (see also character 25). In all *Nephrurus* except some *N. milii*, the tail does not taper evenly but rather has an abrupt constriction one third to three-quarters along its length. In *N. levis, N. milii* and *N. sphyrurus* the proximal, enlarged portion of the tail is quite extensive relative to the narrow terminal portion. All *Nephrurus* (except *N. asper*, which lacks autotomy septa) produce relatively amorphous regenerated tails that are short and bear none of the features characteristic of the original appendages (character 98). Furthermore, in all autotomizing knob-tailed species the cartilaginous rod that typifies lizard regenerates also may be lacking (character 99). Both of these characters are lacking in the outgroups and are deemed derived.

A cartilaginous terminal knob occurs in all species of *Nephrurus* except *N. milii* and *N. sphyrurus*, as well as in *Carphodactylus laevis* (character 100). The presence of this condition in the latter genus has not been previously noted, perhaps because the knob is tiny and few original-tailed specimens have been collected. The knob is best developed in *Nephrurus asper*, in which it is somewhat bilobed (hence the generic name). The function of the knob, if any, remains unknown, although plugging burrow entrances, monitoring mechanical stimuli, and thermoregulation have been suggested (Russell & Bauer 1988). All *Nephrurus* and *Phyllurus* share a further character in the presence of spinose scales on the dorsal surface of the tail (character 101). The primitive condition of smooth or granular scaled tails is seen in all of the East Tasman padded carphodactylines and in *Carphodactylus*, in which the smoothness of the caudal appendage contrasts with the heterogeneous scales of the trunk dorsum.

Several caudal characters also show derived conditions among the padded Carphodactylini. In most gekkonids, and primitively for all tribal and subfamilial groups, the pygal region of the tail tapers gradually into the elongate post-pygal region. This is true of most carphodactylines but in some species a distinct decrease in tail diameter occurs at the pygal/post-pygal border (character 102). This derived state is seen in *Bavayia*

cyclura, in most of the *Rhacodactylus*, and sometimes in *Hoplodactylus chrysosireticus, H. maculatus, H. pacificus, H. stephensi* and *H. delcourti*.

Another character limited to these three genera plus *Eurydactylodes* is the presence of slightly smaller scale rows on original tails that correspond to the level of autotomy septa (character 103). This feature is lacking in *Naultinus* and in *Hoplodactylus rakiurae*.

Kluge (1967b) included tail prehensility as a character in his analysis and reported it present for all of the padded Carphodactylini. He also evaluated the presence of subcaudal lamellae. Prehensility involves a suite of features, some of which have already been discussed. Two further features include the presence of a ventral tail sulcus (character 104), associated with the increase in contralateral muscle bundle mass, and the development of subcaudal lamellae, similar in structure to those under the toes (character 105). The first character is found in *Eurydactylodes* and in *Rhacodactylus leachianus*. Subcaudal scansors were first noted in *Phyllodactylus europaeus* (Fitzinger 1843). The function of these structures has been studied both from the perspective of behavior (van Eijsden 1983) and ecology (Vitt & Ballinger 1982). Subcaudal lamellae occur in all *Rhacodactylus, Eurydactylodes, Bavayia* and *Pseudothecadactylus*. The primitive padless condition occurs in all other carphodactylines. A unique, paddle-shaped tail-·tip, perhaps also associated with prehensility (Guichenot 1866), occurs in *Rhacodactylus ciliatus*.

Reproductive Mode

Character 106: Reproductive mode oviparous (0) or ovoviviparous (1).

Although widespread in squamates as a whole, viviparity is very rare among gekkonids (Kluge 1967a). It occurs only among certain carphodactyline taxa. The plesiomorphic reproductive mode for the Gekkonidae as a whole and more specifically for the Carphodactylini is oviparity, in which two leathery-shelled eggs are laid (Werner 1972; Bustard 1965, 1967a, 1968, 1970). Viviparity has been reported only in the New Zealand genera *Naultinus* and *Hoplodactylus* and in the New Caledonian species *Rhacodactylus trachyrhynchus* (Bartmann & Minuth 1979) (character 106).

Colenso (1880, 1887) first reported viviparity in *Naultinus elegans*. Subsequently all members of this genus have been demonstrated to be live-bearing. Similarly, all *Hoplodactylus* for which reproductive data are available are also viviparous. Reproductive mode is unknown in *H. kahutarae*. Bauer & Russell (1986) postulated that the extinct giant *Hoplodactylus delcourti* was also viviparous. Shine (1985a, 1985b) stated that the reproductive mode of many New Caledonian carphodactylines was unknown. However, literature records exist for egg-laying in *Rhacodactylus chahoua* (Henkel 1981), *R. auriculatus* (Böhme & Henkel 1985), *R. sarasinorum* (Henkel 1986a, 1987, 1988) and *R. leachianus* (Roux 1913; Mertens 1964a). Thus, among *Rhacodactylus*, reproductive mode remains unknown only for *Rhacodactylus ciliatus*. Among the other New Caledonian carphodactylines, all *Bavayia* are oviparous as is *Eurydactylodes vieillardi* (Sauvage 1878), and probably its congener *E. symmetricus*.

The extent of maternal dependence in lizards is difficult to determine. Although much fetal nourishment in live-bearing carphodactylines is derived from yolk, Boyd (1942) reported that the choriovitelline placenta of *Hoplodactylus maculatus* functions "to some extent for food absorption". The ubiquity of viviparity among the New Zealand taxa has lent support to the theory that live-bearing is an adaptation to cold or unfavourable climates. The recent discovery of a tropical live-bearer has shown the need for reconsideration of this hypothesis (see Wake 1977, 1980, 1982 for alternative suggestions about the evolution of viviparity in the Amphibia). Initially proposed by Gadow (1910) and Weekes (1935), this notion has been promoted by most subsequent workers (Neill 1964; Fitch 1970 inter alia). Recently the importance of intermediate stages in the evolution of viviparity has been emphasized (Tinkle & Gibbons 1977; Shine & Bull 1979). Blackburn (1982), Shine (1983a), Shine & Berry (1978) and Shine & Bull (1979) have demonstrated that there are indeed, many more instances of viviparous lizards in cold regions but indicate that this result may primarily reflect differential survival rather than origin of live-bearing under such circumstances. Thus, viviparity might have been a more widespread trait in Eastern Tasman carphodactylines that have survived chiefly in the harsher climatic regime of New Zealand. Despite this possibility, both Blackburn (1982) and Shine (1985a) regarded the distribution of live-bearing among the Carphodactylini to represent a minimum of two independent origins of viviparity.

Fitch (1970), Shine & Bull (1979) and Shine (1985a) have outlined features of biology and ecology that should promote the evolution of live-bearing. Although most of these features are not found in the viviparous carphodactylines (i.e. high demand for nest sites), one is of particular note. Because the female will be burdened by carrying young for a long period of time (up to eleven months in some species), it is essential that she can "afford" not to be exceptionally mobile. Among geckos, most live- bearers, especially *Rhacodactylus trachyrhynchus* and the species of *Naultinus*, are quite slow and deliberate in their movements and both have evolved on land masses free of potential terrestrial mammalian predators.

Defensive Behavior

Character 107: Defensive behavior incorporates back arching and leg extension (0), or lacks these elements (1).

Two states of interspecific defense behavior are seen among members of the Carphodactylini. In some forms the limbs are straightened and extended, the back arched, the tail erected and waved or twitched and the mouth is opened. Frequently this is associated with hissing or vocalizing and may culminate in a lunge at the antagonist. This behavior has been detailed in *Phyllurus platurus* (Mertens 1946; Mebs 1973; Green 1973), *Nephrurus milii* (Bustard 1967b), *N. asper* (Longman 1918; Mertens 1946; Bustard 1967b, 1979; Gow 1979), *N. deleani* (Delean 1982) and *N. levis* (Waite 1929; Bustard 1965) and appears to be typical for all members of these genera. Tail twitching

under unspecified conditions has been seen in *Phyllurus cornutus* (Bustard 1965). Similar actions are performed by members of the genus *Naultinus* (Robb 1980a). *Hoplodactylus granulatus* juveniles may tail-twitch (Angelus 1988), and vocalize, but back arching and leg straightening have not been reported. Rieppel (1973) reported back arching and leg extension in *H. maculatus*, but only during bouts of intraspecific antagonism. Similar patterns of male—male displays have been reported for *Oedura* (Bustard 1965), *Diplodactylus (Lucasium)* (Bustard 1965), *Lygodactylus* (Greer 1967; Kästle 1964), *Phelsuma* (Kästle 1964) and *Coleonyx* (Greenberg 1943).

This set of action patterns has not been reported in connection with interspecific behavior by any of the New Caledonian carphodactylines or by *Hoplodactylus*. Typically, when approached, these taxa will 1) flatten their bodies against the substrate, 2) flee, 3) hiss, growl or croak without a physical display (or with tail waving only), or 4) bite without a preceding display. The defensive behavior of *Carphodactylus* is unknown. The more complex pattern of defense responses is taken to be primitive because it occurs in a variety of gekkonines and, more informatively, is common among the tail-squirting *Diplodactylus* (Bustard 1964, 1969).

RESULTS

Three levels of analysis of the phylogenetic data are presented. The first, which follows here presents the outcome of the PAUP analysis and identifies those derived characters supporting relationships among taxa. The second, an interpretation of these results appears in the discussion. Finally, geological events and a timetable are associated with the phylogeny to yield a scenario of the evolution of the Carphodactylini.

The results of the phylogenetic analysis for full set of taxa and that including the collapsed knob-tailed *Nephrurus* and *Naultinus* (see "Materials and Methods" for a discussion of collapsing these taxa) were similar. The most parsimonious trees generated were 209 steps (consistency index = 0.522) and 186 steps (c.i. = 0.586), respectively. A minimum of 50 most parsimonious trees was generated in each case. Exhaustive searches within the collapsed *Nephrurus* taxa, using the branch and bound option of PAUP, located ten equally parsimonious trees of length 20 and c.i. = 0.650. Use of this option with *Naultinus* yielded more than 200 trees (operation terminated due to limited storage space) of length 6 and c.i. = 0.833.

An Adams (1972) consensus tree, in which competing patterns of branching are represented as unresolved polychotomies, was constructed from the trees generated by PAUP. Twenty subterminal nodes result from the analysis of 38 terminal taxa (Figs. 16-19). Diagnoses of terminal taxa (species) and nodes of "generic" or less inclusive rank are presented under "Systematic Accounts". Basal (suprageneric) nodes are discussed on the following pages.

Two major branches result from the analysis. In the first of these *Phyllurus* was found to be the sister taxon of *Carphodactylus*. These taxa together form the sister group to *Nephrurus* (including those species formerly assigned to the genus *Underwoodisaurus*).
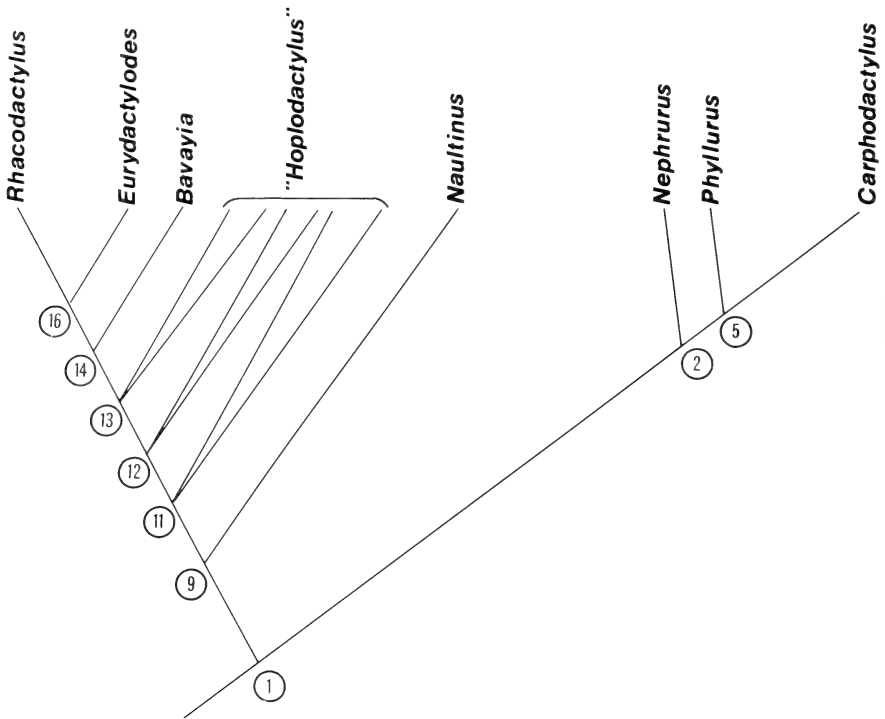
Fig.16: Consensus cladogram of carphodactyline genera. The subgenus *Pseudothecadactylus* is included within *Rhacodactylus*. Numbers of nodes referred to in the text are circled in this and subsequent figures.

In the second major clade *Pseudothecadactylus* forms part of *Rhacodactylus*, which is the sister taxon of *Eurydactylodes*. *Bavayia* is the sister taxon of this group. Subsequent outgroups include three pairs of species of *"Hoplodactylus"*, each forming a trichotomy (Fig. 18). *Naultinus* is the sister taxon of *"Hoplodactylus"* plus the New Caledonian carphodactylines (and *Pseudothecadactylus*) (Fig. 16).

Diagnoses of the suprageneric nodes are in telegraphic form and include all of the changes of character state that occur at a given node as supported by the consensus cladogram. The numbers of the characters applicable at each node follows parenthetically. Character state reversals may be distributed in several different patterns on the cladogram and such characters may be more inclusive than indicated by the diagnoses. Reversals between nodes are indicated by semi-bold figures. Uniquely derived character states are followed by an asterisk (*). Autapomorphic characters not included in the analysis are also included in the diagnoses and external characters are stressed over osteological features.

Node 1

This grouping corresponds to the Carphodactylini in its entirety (Fig. 16). Taxa united at this node share the following character states derived relative to the outgroup node: extreme overlap of jugal and lateral infraorbital process of prefrontal; inner ceratohyal process present; autotomy planes absent in at least some pygal vertebrae; preanal organs in a triangular patch*. (13, 18, 28).

Node 2

The taxa united at Node 2 (Fig. 17), correspond to the group of padless Australian carphodactylines *(Carphodactylus, Nephrurus, Phyllurus)* and primitively share the following derived character states: premaxillae completely unfused; parietal short and very broad; coronoid-dentary suture anterior to dentary-surangular suture; teeth minute and extremely numerous; hyoid cornu with antero-medial process reduced and postero-lateral process large and hooked; lumbar vertebrae two (rarely three) in number; caudal vertebral centra extremely short; post-pygal pleurapophyses absent or greatly reduced; metischial process expanded; hypoischium slender and elongate; metatarsal V only slightly hooked; extra-brillar fringe large, thick, with brown spot on internal face; external ear aperture large and vertical; dorsal trunk scalation consisting
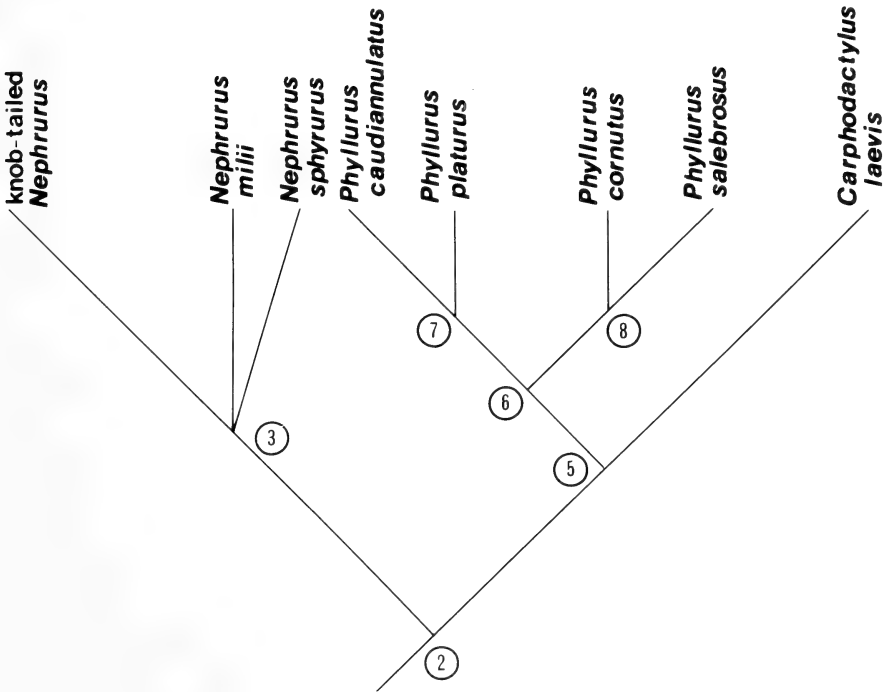

Fig.17: Consensus cladogram of the Australian padless carphodactyline genera. See text for characters at each node.

of tubercles surrounded by rosettes of scales; preanal organs absent; cloacal spurs consisting of clusters of conical scales; tail short and pyramidal; dorsal tail scalation spinose. The polarity of the states of characters 16, 50 and 54 could not be assessed, but among the Carphodactylini occur in all species united at Node 2 and in no others. Character 96 undergoes one reversal and characters 92 and 101 undergo at least two reversals or may have evolved independently outside of node 2 (in *Rhacodactylus cavaticus*). (2, 8*, 16-B, 17*, 18*, 26*, 27*, 49*, 50-A, 54-A, 68*, 69*, 92*, 94*, 96*, 101-B).

Nodes 3 and 4

See *Nephrurus* in systematic accounts.

Node 5

The taxa united at Node 5 correspond to the group including *Carphodactylus laevis* and all the species of *Phyllurus* and form a monophyletic group, the members of which primitively share the following set of characters: dorsal skin of head co-ossified with skull; nasal bones elongate and narrow; supraoccular portion of frontal deeply furrowed or concave; posterior border of parietals complete, roofing entire occipital region of skull; squamosal large and relatively broad; clavicular fenestrae minute or absent; metatarsals V and IV shortest. Characters 1, 7 and 11 arise in parallel in several other carphodactyline lineages. Characters 5 and 7 undergo reversals at less inclusive nodes. (1, 3*, 5, 7, 11, 42*, 52*).

Nodes 6—8

See *Phyllurus* in systematic accounts.

Node 9

The taxa united at Node 9 correspond to the East Tasman group of padded carphodactylines (*Naultinus, Hoplodactylus, Bavayia, Eurydactylodes* and *Rhacodactylus* including *Pseudothecadactylus*) and primitively share the following character states: fronto-parietal suture curved; scleral ossicles fewer than 30; coronoid dentary suture at same level as dentary-surangular suture; one lumbar vertebra; pygal pleurapophyses markedly decreasing in size distally; metatarsals III and IV parallel; lateral pair of cloacal bones present; tongue and lining of mouth distinctly pigmented; peritoneum pigmented jet black; digital lamellae with scansorial setae; scales of cloacal spurs pointed, two or more in number; dorsal tail scales granular; live-bearing. Reversals occur in characters 9, 15, 59, 63—66, 95 and 106. The derived character state 15 also appear independently at several places within the padless lineage. Character 59 is variable in the taxa *Hoplodactylus duvaucelii, H. maculatus* and *H. pacificus*. (9-B, 15, 16-A, 23, 24-A, 57*, 59, 63, 64, 65, 66-B, 72*, 101-A, 95, 106).

Node 10

See *Naultinus* in systematic accounts.
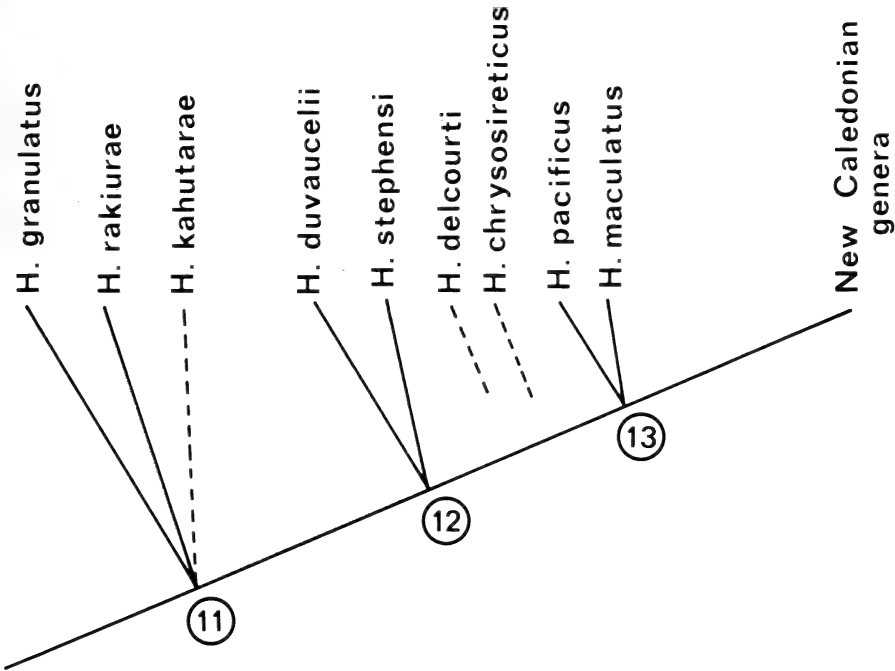
Fig.18: Consensus cladogram of the species of the paraphyletic metataxon *Hoplodactylus*. Species connected by dashed lines were not included in the initial phylogenetic analysis.

Node 11

The taxa united at this node correspond to the group of padded carphodactylines exclusive of *Naultinus* (Fig. 18) and primitively share the following character states: overlap of jugal and lateral infraorbital process of prefrontal narrow or excluded; inner proximal ceratohyal process absent; zero or one inscriptional ribs; three to four abdominal ribs; autotomy planes present in all post-pygal vertebrae; metatarsal length (shortest to longest) V-I-II-IV-III; dorsal body scalation homogeneous; webbing between digits II-III-IV; smaller scale rows on tail corresponding to level of autotomy septa; defensive behavior without sterotyped tail wave and lunge. Characters 13, 19 and 28 all undergo reversals at this node. Character 78 appears in parallel in two species of *Naultinus* and undergoes later reversals within node 18. (**13**, **19**, **28**, 32-A, 33-B, 53*, 78, 88*, 103, 107*).

Node 12

The New Caledonian carphodactylines, *Rhacodactylus (Pseudothecadactylus)* and *Hoplodactylus* exclusive of *H. rakiurae, H. granulatus* and probably *H. kahutarae* are

united by the following characters: mesosternal extension present, color of mouth lining pale pinkish, scansorial pads broadly dilated. Character 31 undergoes a reversal at node 16. (31, **64**, 73*).

Node 13

The taxa at node 12 exclusive of *Hoplodactylus stephensi* and *H. duvaucelii* and perhaps *H. chrysosireticus* and *H. delcourti* (the latter two taxa may be diagnosed at node 14), are united at Node 13 and primitively share the following characters: color of tongue pale pinkish; peritoneal pigmentation present, scattered; pygal region of tail abruptly decreasing in diameter to that of pygal region; scales of cloacal spurs rounded, 1—5 in number. Character 102 undergoes several subsequent reversals and character 63 may apply at the more inclusive node 12. (**63**, 66-A, 95, 102).

Node 14

The New Caledonian taxa plus *Pseudothecadactylus*, united at Node 14 (Fig. 19), primitively share the following characters: overlap of jugal and lateral infraorbital process of prefrontal extensive; recessus scalae tympanii at least partially hidden ventrally by lateral process of basioccipital; scleral ossicles 30 or more in number; peritoneum unpigmented; subcaudal scansors present; oviparous. (**13**, 14*, **15**, **65**, 105*, **106**).

Node 15
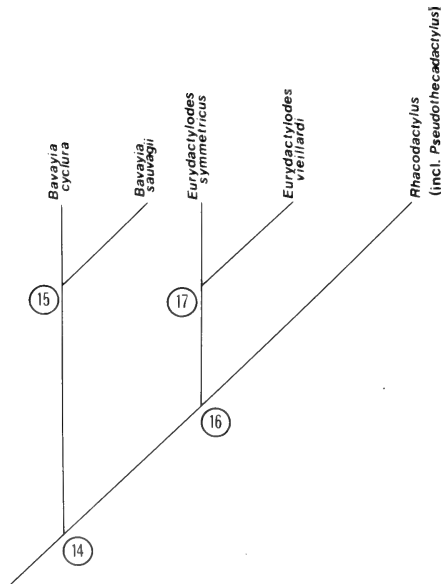
See *Bavayia* in systematic accounts.

Fig.19: Consensus cladogram of the New Caledonian carphodactyline geckos. See text for characters at each node.

Node 16

This node unites the group including *Eurydactylodes, Rhacodactylus* and *Pseudothecadactylus*, the members of which primitively share the following characters: mesosternal extension absent; infralabial scales deeper than broad; folds of loose skin on posterior face of hindlimb. Character 90 undergoes two reversals in species of *Rhacodactylus*. **(31,** 86*, 90).

Node 17

See *Eurydactylodes* in systematic accounts.

Nodes 18 and 19

See *Rhacodactylus* in systematic accounts.

Node 20

See *Rhacodactylus (Pseudothecadactylus)* in systematic accounts.

DISCUSSION

The phylogenetic analysis supports a primary division of the Carphodactylini into a primitively padless Australian clade (Node 2) and a padded Tasmantis clade (Node 9). This division is supported by pedal characters, cranial and axial skeletal features and characters of scalation. The padless lineage is especially well-supported with eleven uniquely derived features. An additional character not included in the analysis — the presence of setules on cutaneous sensilla (Bauer & Russell 1988) — also appear to support this group. Fifteen shared character states support the padded group but only ten of these are known to be derived and only two are synapomorphies unique to all members of the clade.

Within the padless lineage the consensus tree yields a secondary division into the *Nephrurus* clade (Node 3) and the *Phyllurus—Carphodactylus* clade (Node 5). A number of characters are shared among some members of the two clades but the dichotomy is unequivocal and both lineages are supported by three uniquely derived states. Three additional characters support each of the subdivisions of the latter group. *Phyllurus* is divided into two clades of two species each. The first contains the smaller "leaf-tails" *(P. caudiannulatus* and *P. platurus)* (Node 7) and the second, the larger forms *P. cornutus* and *P. salebrosus* (Node 8). Both clades are supported by osteological synapomorphies.

The genus *Nephrurus* (Node 3) is reduced into three unresolved branches (Fig. 17): the knob-tailed species (Node 4), *N. milii* and *N. sphyrurus*. The last two species were formerly placed in the genus *Phyllurus* (Kluge 1967b; Russell 1980) or were accorded

generic rank as representatives of *Underwoodisaurus* (Wermuth 1965; Cogger 1975b, 1979, 1983) (see synonymy), which was assumed to have close affinities with *Phyllurus*. The results of the analysis, however, support the association of these two species with *Nephrurus*, rather than with the leaf-tails. This relationship is also supported by the fine structure of integumentary mechanoreceptors not dealt with in this analysis (Bauer & Russell 1988). It appears that Waite (1929) was among the only workers to recognize the similarity between *milii* and the knob-tailed geckos and to hint at some relationship. This relationship is supported by features such as an expanded brillar fringe and a short, pyramidal tail. *Nephrurus milii* and *N. sphyrurus* lack the knob- tail, spinose toe surfaces and reduced phalangeal formulae of their congeners, but these are plesiomor-phic features. Further, microcomplement fixation work by Baverstock (King 1987a, 1987b) also supports this affinity, suggesting an approximate divergence time of 7 my between *N. milii* and *N. laevis* versus 23—26 my between *N. milii* and *Phyllurus* spp.

Although the consensus cladogram (Fig. 17) depicts a trichotomy above Node 3, it is possible that future work will indicate that *N. milii* and *N. sphyrurus* are each others closest relatives, forming a monophyletic group with the knob-tailed geckos as their im-mediate sister group. In this case the retention of the generic name *Underwoodisaurus* would be recommended. As a phylogenetically conservative measure I have included all of the taxa in the genus *Nephrurus*, pending more detailed analysis of relationships within the clade. Regardless, the generic name *Phyllurus* should not be used for the species *milii* and *sphyrurus* as this would make *Phyllurus* polyphyletic. Within the knob-tailed *Nephrurus* (Node 4), no resolution was possible, although some patterns of relationship were suggested by particular sets of the original cladograms generated. In particular, the "spiny" knob-tails, *Nephrurus asper* and *N. wheeleri*, are probably each others closest relatives and represent the sister taxon of the "smooth" knob-tails, which are united by a further digital reduction and many other characters. Similarity of scalation suggests affinities between *N. levis* and *N. vertebralis* and between *N. stellatus* and *N. deleani*. The consensus resolution into a polychotomy is primarily bas-ed on several homoplastic features, such as co-ossification, which tend to unite the larger species *N. asper* and *N. levis*.

The first division within the Tasmantis lineage (Node 9) suggests the divergence of the members of the genus *Naultinus* (Node 10) from the remaining taxa. The eight species of *Naultinus* are morphologically similar and share the uniquely derived character states of weakly ossified girdles, green pigmentation and smooth-sided, vertical pupils and diurnality. No resolution within the genus was suggested by the analysis although each species may be diagnosed using a variety of external characters. The genus *Heteropholis*, resurrected by McCann (1955) for the South Island green geckos, appears to have no genealogical reality. No division into North and South Island components is suggested and it seems unlikely that the addition of the taxa not included in the initial analysis, *N. manukanus, N. tuberculatus* and *N. poecilochloris*, would provide any ad-ditional resolution.

Bull & Whitaker (1975) and Thomas (1982b) suggested that *Naultinus manukanus* and *N. rudis* are sister taxa and that *N. tuberculatus* and *N. stellatus* perhaps also form a

species pair. In turn *N. poecilochloris* has been regarded as intermediate between the other forms that surround its geographical range. Rare wild hybrids of some of the adjacent species pairs are known (Bull & Whitaker 1975) and all of the species will freely interbreed in captivity (Meads 1982). However, breeding seasons in the wild are generally somewhat asynchronous, suggesting some degree of premating isolation. In addition, the species are largely allopatric, although in the northern South Island, the ranges of several species approach one another or overlap slightly.

The overall patterns suggest a recent radiation of the genus *Naultinus*, with some behavioral but little morphological divergence. Electrophoretic analysis might be useful in elucidating relationships within the group, for few morphological features of determinable polarity were discerned. I accept the validity of all of the generally recognizable species, largely on the grounds of coloration differences and reproductive timing, but many or all of the species may be involved in a Rassenkreis, similar to that of the plethodontid salamander *Ensatina eschscholtzii* (Stebbins 1949, 1957; Brown 1974; Wake & Yanev 1986; Wake et al. 1986).

The taxon *Hoplodactylus*, consisting of nine species (one believed to be extinct), is paraphyletic, with some members more closely related to the New Caledonian carphodactylines (Node 14) than to other *Hoplodactylus*. With three taxa excluded from the analysis *(H. chrysosireticus, H. delcourti* and *H. kahutarae)*, three levels of polychotomous branching within the genus were identified and the resultant patterns of relationship are tentative at best. The group as a whole (Node 11), including the New Caledonian genera, is supported by ten characters, three of which are uniquely derived: relative metatarsal length, digital webbing, and absence of a stereotyped defensive behavior. *Hoplodactylus rakiurae* and *H. granulatus*, and probably *H. kahutarae*, are sister taxa to Node 12, which is supported by the single uniquely derived feature of broadened scansorial pads. The consensus cladogram also suggests that *H. duvaucelii* and *H. stephensi* are sister taxa to the remaining species (Node 13) and that *H. maculatus* and *H. pacificus* are part of a trichotomy also involving the monophyletic New Caledonian group. No uniquely derived characters support the relationship of *Hoplodactylus maculatus* and *H. pacificus* to the New Caledonian carphodactylines. Rather, I consider it likely that all of the species which branch at nodes 12 and 13 plus *H. chrysosireticus* and *H. delcourti* form a monophyletic group of broaded-padded *Hoplodactylus* which, as a whole, forms the sister taxon of the New Caledonian species. On the basis of external characters of unknown polarity *H. pacificus* and *H. stephensi*, and *H. maculatus* and *H. chrysosireticus* appear to be affiliated, although it is possible that *Hoplodactylus maculatus* as now construed is a paraphyletic species complex. *Hoplodactylus* thus is holophyletic but not monophyletic. I propose that use of the name be maintained until relationships within the subgroupings are resolved and two or more natural groups may be demonstrated.

It is somewhat surprising that the New Caledonian species appear to have arisen from within the New Zealand stock, as this would suggest that live-bearing has been evolved and subsequently lost (and regained in *Rhacodactylus trachyrhynchus*). Although there is no reason to assume that live-bearing, especially ovoviviparity, cannot undergo a

character state change to oviparity, the current dogma would not seem to allow it (see **reproductive mode** in character analysis).

Node 15 diagnoses the genus *Bavayia* with five characters, among them uniquely deriv-ed, long, nearly complete second ceratobranchial arches. Node 16 diagnoses the remain-ing carphodactylines, which are supported by three characters, including the uniquely derived condition of infralabials deeper than broad. The two major divisions within this clade are the genera *Eurydactylodes* (Node 17) and *Rhacodactylus* (Node 18). *Eurydactylodes* possesses many apomorphic characters and is one of the most mor-phologically distinct of all gekkonid lizards. *Rhacodactylus* includes both, the giant New Caledonian forest geckos and the Australian geckos formerly referred to the genus *Pseudothecadactylus* (Node 20).

"Pseudothecadactylus" is diagnosed from other *Rhacodactylus* by the absence of a claw on digit one and by divided subdigital scansors. Although it was not entered into the analysis, *"P". cavaticus*, based on external morphology, is assumed to be most closely related to *"P." lindneri*. These species in turn form the sister group of *P. australis*. Among the New Caledonian species only one subgrouping was supported by the consensus tree, that uniting *R. ciliatus* and *R. chahoua*. Nevertheless, the majority of the original trees produced suggested that *Rhacodactylus auriculatus* is the sister tax-on of all other members of the genus and that *R. leachianus* is the sister taxon to the *R. ciliatus/chahoua* group. *Rhacodactylus sarasinorum, R. trachyrhynchus* and the Australian species are successively remote sister groups of these taxa. As used throughout this paper, the name *Pseudothecadactylus* should be relegated to subgeneric status in order to maintain the monophyly of *Rhacodactylus*. In addition to the mor-phological evidence supporting this suggestion, King (1987a) found that *Pseudo-thecadactylus* shares a derived chromosomal morphology with *Rhacodactylus*. These results contradict Cogger's (1975a) conclusions that *Pseudothecadactylus* is an ancient group with relict distribution in northern Australia.

With the exception of the segments of the cladogram dealing with the species currently assigned to *Hoplodactylus*, the hypothesis of relationship among the carphodactylines is moderately robust and provides resolution at least at the generic level. These results differ in several ways from the hypothesis put forward by Kluge (1965a, 1967a, 1967b). Although Kluge recognized the unity of padless forms, he suggested that *Nephrurus* and *Phyllurus* were sister taxa and that *Carphodactylus* was the sister taxon of these two genera combined. He also placed both *Nephrurus milii* and *N. sphyrurus* in the genus *Phyllurus*.

Kluge's (1965a, 1967b) placement of *Pseudothecadactylus* as the immediate sister group to the remaining padded taxa is also contradicted. My hypothesis is, however, in accord with Russell's (1972) views of *Pseudothecadactylus*, in part because the polarity of some toe characters was established on the basis of Russell's work. Other intra-Caledonian relationships are similar to those proposed by Kluge. On the other hand, Kluge (1965a, 1967b) regarded the New Caledonian group as a whole paraphyletic because it gave rise to the New Zealand species. The reverse has been found in this study, and the genus *Hoplodactylus* is seen as a paraphyletic group. It is probable that

Kluge's views were in part due to the belief that ovoviviparity had only arisen once in the Gekkonidae and that a reversal to oviparity was unlikely. Kluge (1967b) also considered *Hoplodactylus* and *Heteropholis* to be each other's closest relatives. It has since been demonstrated that *Naultinus* and *Heteropholis* should be synonymized (Meads 1982; Thomas 1982b; this study), and the synonymy of all species of *Heteropholis* and *Naultinus* has even been proposed (Meads 1982; Gill 1986).

Aspects of the phylogenetic hypothesis are also supported by independent sets of data from other sources. Recent studies of karyology by King (1987a, 1987b, 1988) suggest that the Carphodactylini plus *Oedura* form a monophyletic group. The placement of *Oedura* has not been addressed in this study but again raises persistent questions about carphodactyline monophyly that need to be addressed in the context of a broader systematic work. Immunological work in progress (Rainey & Bauer, in prep.) also provides some support for the hypothesis, but this is too tentative at present to serve as a test of the hypothesis. Data regarding the geological history of the southwest Pacific, however, are plentiful and internally corroborated, and should serve as a means to evaluate, if not test, the phylogenetic hypothesis.

BIOGEOGRAPHY OF THE CARPHODACTYLINI

The modern approach of biogeographical analysis has been (or should be) characterized as a mixture of vicariant and dispersalist philosophies (McDowall 1980; Murphy 1983). Dispersal and equilibrium faunal exchange have historically been regarded as the prime determinants of species number and diversity of islands (MacArthur & Wilson 1963, 1967). It now appears that paleogeographical legacy is more important in determining faunal composition in at least some situations (e.g. Lawlor 1986 for Indo-Australian mammals and Gardner 1986 for lizards of the Seychelles). The importance of paleogeographical factors increases with island age and isolation, and is greatest for groups of organisms with low vagility. Furthermore, the effects of paleogeological events on the compositions of island faunas should be reflected in the phylogenies of many groups of organisms (Nelson & Platnick 1981). Dispersal events can and do occur in nature, they are difficult to corroborate with independent sources of data (although Murphy 1983 has applied genetic distance techniques to this question). The ad hoc nature of most dispersalist arguments does not affect the likelihood that such events are responsible for the distribution of animal groups, but it does make such arguments difficult to support. For this reason I have used vicariance biogeography as my initial method of evaluating the phylogeny of the Carphodactylini hypothesized in the preceeding section.

I use two approaches of paleobiogeography which may be useful in examining the phylogenetic hypothesis of carphodactyline relationships. The first is the search for reciprocal illumination between phylogenetic and geological hypothesis. Congruence of implied biogeographical pattern (e.g. of taxon-area cladogram and geological-area

cladogram) supports both hypotheses (but is not testable). The second approach is that of "cladistic biogeography" (Humphries & Parenti 1986) in which patterns of phylogeny of many groups or organisms yield hypotheses of common biogeographical pattern. Again, corroboration of a given phylogeny may be obtained by congruence of implied biogeographical relationships to that of the generalized hypothesis. Although the general hypothesis is perhaps falsifiable (Kirsch 1984), individual phylogenies cannot be falsified by non-congruence with the general pattern. Rosen's (1976) arguments regarding falsifiability of biogeographic hypotheses are circular. If neither the phylogenies of the organisms nor the geological histories of the areas involved in a particular distributional track are "known", non-congruence is at best a falsification of one (but which?) of the biological or geological hypotheses.

Despite certain limitations of the method, I accept the logical hegemony of vicariance over ad hoc dispersalist hypotheses and propose that for the southwest Pacific, where geological data are abundant and largely verified by numerous techniques, a meaningful evaluation of the phylogenetic hypothesis can be made by
1) an examination of the degree of reciprocal illumination provided by the phylogenetic and geological data sets and
2) the application of the cladistic biogeographic method.

Unfortunately the number of taxa inhabiting the region for which phylogenetic hypotheses exist is small. I shall therefore concentrate on the comparison of phylogenetic and geological data sets.

My interpretation of the major events in the history of the southwest Pacific region is largely derived from recent general works on the Pacific Basin, as well as more technical regional geological studies. The following works have been particularly useful: Keast 1981; Packham 1973; Lewis 1980; G.R. Stevens 1977, 1980a, 1980b; Lillie & Brothers 1970; Griffiths & Varne 1972; Hayes & Ringis 1973; Smith et al. 1973; Paris 1981; Archer & Clayton 1984; Holloway 1979; Coleman 1980; Raven & Axelrod 1972; Recy & Dupont 1982; Briggs 1987.

Evaluation of the Phylogenetic Hypothesis

The hypothesis of carphodactyline relationships based on morphological synapomorphies is evaluated by comparison to the presumed geological history of the regions associated with the distribution of the taxa. A simplified consensus cladogram depicting the hypothesis of relationships, is shown in (Fig. 20a). This, in turn is translated into a taxon-area cladogram by substituting the regions occupied for each taxon (Fig. 20b). Some of the ranges have been simplified and represent the distribution of each taxon as a whole, excluding parts of the ranges of single species if they fall far outside the primary distribution of the higher order taxon. Thus, although *Nephrurus milii* and *N. sphyrurus* occur (in part) in eastern Australia, the genus *Nephrurus* has been replaced by the area "Western Australia". Similarly, in New Zealand, the wide-ranging *Hoplodactylus granulatus* and *Hoplodactylus maculatus* have been assigned to the
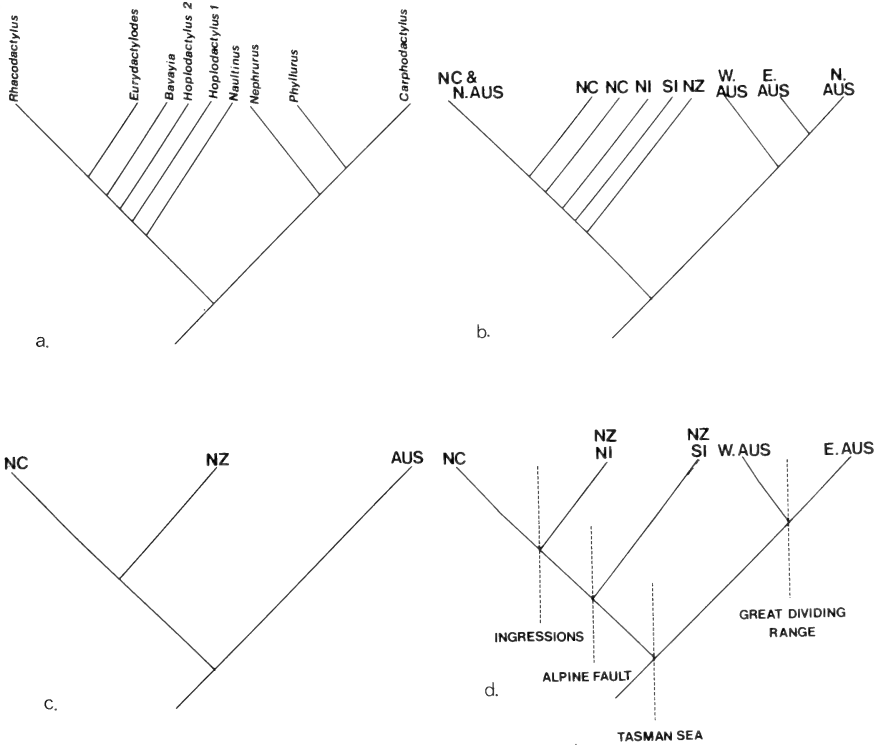
Fig.20: Test of the phylogenetic hypothesis. (a) Simplified consensus cladogram of the Carphodac-tylini. (b) Area cladogram derived from A (NC = New Caledonia, AUS = Australia, NI = North Island, New Zealand, SI = South Island, New Zealand, NZ = New Zealand). (c) Simplified pat-tern of geographical relationships derived from geological data. (d) Modified geographical pattern of relationships derived from geological data. Note the similarities between b and d.

South Island and North Island respectively, on the basis of the distribution of the other members of the clades of which they are a part.

A simplified tree of geological relationship for the areas involved is presented in Fig. 20c. In this diagram New Caledonia and New Zealand are shown as sister areas. This primary division from Australia is the result of the opening of the Tasman Sea while the division between the two island groups is the result of the sinking of the Lord Howe Rise and subsequent marine ingressions. The first event is conclusively dated to 80 mybp, but the second is less accurate, because effective contact may have been lost at any time before the Oligocene. At least sporadic contact was probably likely until that time (Dawson 1986), although a date as early as 65 mybp is possible.

This reconstruction, however, treats New Zealand as a single entity. In fact, New Zealand seems to have been divided since at least the time of the Tasman split, except

for brief periods during the Pleistocene glaciations. It is unclear exactly which areas of New Zealand were emergent during the entire period of time since the opening of the Tasman barrier, but the components of both the Pacific and Australo—Indican plate blocks of New Zealand were relatively distant during much of the period between the initiation of movement along the Alpine Fault and the Miocene. The earlier event corresponds to the earliest Paleocene.

A more accurate reconstruction of the relationships among land masses in the southwest Pacific may be made based upon the composite structure of New Zealand (Fig. 20d). The first split in this figure corresponds to the opening of the Tasman Sea and the separation of Australia from the Tasmantis block. Within Australia an orogenic event, the raising of the Great Dividing Range, occurred in the Paleocene, coincident with the subduction of the Pacific Plate under the Australian crust as a result of the counter-clockwise rotation of New Zealand. Concurrently in New Zealand, movement was initiated along the Alpine Fault, and emergent portions of the southern block (= Torlesse terrane) began a long period of isolation from the northern, Australian Plate terranes of New Zealand. The latter retained sporadic northern contacts along the Inner Melanesian Arc. Later, probably as a result of Oligocene marine ingressions, New Zealand and New Caledonia lost the contact that had previously been provided by emergent land and narrow water gaps along the Lord Howe Rise and/or the Norfolk Ridge.

This reconstruction corroborates the phylogenetic hypothesis of relationships among the Carphodactylini in its broad outline, especially with regard to the nodes corresponding to the Australian padless genera (Node 2, Fig. 16), the genus *Nephrurus*, the genera *Phyllurus* and *Carphodactylus* (5), the Tasmantis (padded) genera (9), the New Caledonian genera plus the northern *Hoplodactylus* (12), and the New Caledonian genera alone (14). In each of these cases, a known vicariant event corresponds to a cladogenic event and provides a putative explanation for the origins of allopatry and subsequent divergence of the lineages involved. Each case is discussed in more detail in the scenario for the evolution of the Carphodactylini that follows. Other portions of the phylogenetic hypothesis, including division between *Phyllurus* and *Carphodactylus* and the distribution of *Pseudothecadactylus* (i.e. some *Rhacodactylus*) in Australia, are not corroborated by this geologically-derived geographical pattern of relationships. In these instances, more detailed geographical hypotheses should be examined.

When geographical hypotheses are lacking it may be possible to obtain corroboration (although not falsification) of the phylogenetic hypothesis by referring to taxon-area relationships in other, unrelated organisms. Unfortunately, this method can rarely be applied with success because it is only useful when genealogical relationships within these other taxa are known. However, the congruency of several taxon-area relationships suggests a generalized track (sensu Croizat 1958, 1964) which in turn implies commonality of distributional cause, i.e. a pattern reflecting vicariance. Repeated generalized tracks thus indicate that geological data may support paleogeographical reconstructions which are consistent with hypothesized patterns of cladogenesis. Certain patterns

of carphodactyline relationships not addressed by the coarse-grained geological comparison are supported by the corroboration of congruent patterns of taxon-area relationships in other taxa. In particular, Cracraft (1986) demonstrated that a clade of northern Australian chestnut-shouldered wrens *(Malurus)* share the same pattern of species-area relationships as *Rhacodactylus* (subgenus *Pseudothecadactylus*), i.e. northern Cape York Peninsula + (Arnhem Land + Kimberley Plateau). The same pattern is also found in the finch *Poephila personata* (Arnhem Land + Kimberley Plateau) and its sister species *P. leucotis* (Cape York) and in many other bird groups (Ford 1978; Cracraft 1986). Similarly, the association of the Atherton Plateau with the eastern forest belt of coastal Queensland and New South Wales, as suggested by the relationship of *Carphodactylus* and *Phyllurus*, is corroborated by the distributions of sister taxa within the avian genera *Tregellasia* and *Ptiloris* (Cracraft 1986).

Details of the phylogenetic hypothesis dealing specifically with the carphodactylines of New Zealand require more attention. The ranges of many of the 17 gecko species that occur there are complex. Furthermore, the phylogenetic hypothesis within *Hoplodactylus* is weak. The geology of the areas involved is well studied but the correlation of paleoposition with emergent land is not exact enough to provide a sound basis for corroboration of any but the primary north/south division following the initiation of plate rotation. Corroboration of the hypothesis of carphodactyline relationships by taxon-area congruence must also await phylogenetic analyses of other New Zealand groups.

Details of the phylogenetic hypothesis as they relate to intra-island distributions remain untested by geological data, but division of the Carphodactylini into regional groupings receives support from paleogeography and suggests that cladogenesis within the group is associated with vicariant events in the Late Mesozoic or Early Tertiary.

The Traditional View of Carphodactyline Evolution and Biogeography

Underwood (1957) proposed a scenario for the arrival in Australia of the various gekkotan groups, but did not deal with the events in Tasmantis. He suggested that pygopodids were the first invaders of Australia, with diplodactylines following shortly thereafter. *Phyllodactylus* (recognized by Underwood to be worldwide in its distribution) was the next to enter, followed finally by the ancestors of the remaining Australian gekkonines. Kluge (1965a, 1967a, 1967b) first proposed a scenario for the evolution of the Carphodactylinae as a whole. Like Underwood, Kluge worked in a pre-tectonic, dispersalist framework; thus he did not consider the theory of continental drift "germane to a discussion of the zoogeography of the Gekkonidae, particularly the Diplodactylinae". Furthermore, Kluge's hypotheses of relationship were pre-Hennigian — based not upon shared derived features, but on the percentage of primitive relative to derived features, with primitiveness not always demonstrated. (It should be noted that Kluge (1987) has revised his evaluation of the evolution of higher order gekkonid taxa using plate tectonics as a basis, although he does not provide a new scenario for the evolution of the Carphodactylini.)

Kluge (1967a) stated that geckos arose in the Upper Jurassic or Lower Cretaceous (based upon the dating of *Ardeosaurus*, now rejected by Kluge 1987 as not demonstrably gekkotan). The Eublepharinae, circum-global in distribution, were considered to show a relict pattern of extant forms, of which the most primitive genus was *Aeluroscalobotes*. By virtue of its occurrence in Borneo and South East Asia, *Aeluroscalobotes* fits well with Darlington's (1948, 1957) views of the Old World tropics as the center of reptilian origins. By the Tertiary, proto-*Coleonyx* had entered the Americas via the Bering Land Bridge. Kluge proposed that diplodactyline ancestors evolved in southeast Asia during the late Mesozoic and dispersed through the Indo—Australian Archipelago to Australia, where they subsequently replaced any pre-existing eublepharines. By the end of the Maestrichtian, the diplodactyline stock had crossed a broad land connection south into Australia (the Sumatran migration tract of van Steenis 1934a, 1934b, 1936), where they continued to evolve in isolation. Rising sea levels in the upper Eocene and later in the Pliocene cut off Australia from New Guinea, where diplodactylines were replaced by gekkonines. These had probably evolved at the same time as diplodactylines, and first radiated westward into Africa. New World gekkonines and the Sphaerodactylinae reached America by rafting; the latter stemmed from a *Lygodactylus*-like ancestor in the early Tertiary.

Kluge's (1967b) more detailed scenario for the evolution of the Carphodactylini was based largely upon prevailing views that there had never been any trans-Tasman land connections (Flemming 1962), although he did accept links from Australia to New Caledonia. Kluge considered the center of the Carphodactyline radiation to be in northeastern Australia and New Guinea in the paleotropical Tertiary flora (Burbidge 1960). Major radiations within the Carphodactylini occurred along the New Zealand migration tract (Burbidge 1960) from the center in Queensland to New Caledonia and the Loyalty Islands and thence to New Zealand. Kluge proposed that the New Zealand species were derived from near the basal stock of the New Caledonian species and that they reached New Zealand in the Miocene. Thus ultimately, Kluge (1967a, 1967b) accepted a Malaysian origin for the Diplodactylinae, similar to that proposed for most of the principal plant groups.

The carphodactyline/diplodactyline split was associated with the Tropical and Eremean floral zones, respectively (or Toressian and Eyrean zones) (Kluge 1967b). The Diplodactylinae evolved primarily in association with arid regions and later invaded the Toressian and Bassian mesic zones. Likewise, the Carphodactylini in Australia remained in association with the eastern forests, with some *Nephrurus* invading the Eyrean deserts. Neither group successfully invaded the cooler southeastern Bassian region of Victoria or Tasmania.

Kluge's scenario was a reasonable reconstruction, given the geological knowledge available and accepted by mainstream biologists (Darlington 1957, Solem 1959 and Caughley 1964 had earlier suggested similar dispersal routes). Unfortunately, as the reality of the tectonic development of the region became known, few workers abandoned this analysis. Cogger & Heatwole (1981) provided a tectonic overview by way of introduction, but retained Kluge's biogeographical hypothesis even though the paleoposi-

tions of Asia and Australia in the late Mesozoic would have precluded the type of dispersal that Kluge advocated (Cracraft 1975).

Bull & Whitaker (1975) also maintained Kluge's Miocene date for the entry of geckos into New Zealand, and as recently as 1986 Robb (1986) maintained that "lizards evolved much more recently than *Leiopelma* and *Sphenodon*, and would not have spread to Gondwanaland before it broke up". Robb (1986) further contended, as Kluge did, that the geckos arrived from the north, via New Caledonia. Thus, while she acknowledged the tectonic framework of the southern continents, she favored a scenario based on pre-tectonic geology. Acceptance of the ramifications of tectonics would also solve the problem of the absence of snakes in New Zealand and New Caledonia (Robb 1973) because they imply that the Tasman Sea opened long before snakes appeared in Australia (Smith 1973).

Recently, however, many workers (Tyler 1979a; Cracraft 1980; Flannery 1984; Gibbons 1985; Kluge 1987) have recognized the inconsistencies of maintaining Kluge's (1967b) scenario in light of current geological knowledge and have proposed a Cretaceous spread of the Diplodactylinae in the southwest Pacific before the isolation and breakup of Tasmantis. Tyler (1979) went as far as to suggest that the Diplodactylines may have been the only squamates in Australia in the Eocene. In New Zealand, Towns et al. (1985) have also questioned the proposed age of the scincid fauna and have advocated biochemical methods as a means of gauging approximate ages of lineages. King (1987a, 1987b) has proposed a detailed scenario for the biogeographic history of the Diplodactylinae on the basis of karyological and immunological evidence. In general, the application of such techniques to phylogenetic problems in Australia and the Pacific has pushed back divergence times from the Pleistocene to the mid-Tertiary (e.g. Maxson et al. 1982; Maxson & Roberts 1985), in accordance with known geological events. The following reconstruction of the evolution of the Carphodactylini is based on the historical geological reconstruction of the southwest Pacific as outlined above and suggests a possible scenario for the evolution of the group as a whole.

A Scenario for the Evolution of the Carphodactylini

The primary division of the Diplodactylinae into the Diplodactylini and Carphodactylini cannot be clearly related to a single vicariant event. The period 140—120 mybp was a time of continental lake systems in Australia. These lake systems, along with occasional marine ingressions from the east, may have been associated with this division. Likewise, the origin of the Pygopodidae probably dates from the Mid-Cretaceous and cannot be associated with a particular tectonic event.

By the close of the Rangitata Orogeny, the eastern margin of Gondwana (the incipient Tasmantis) had been raised and remained near or in contact with Australia until 90—80 mybp. In the intervening 30—40 my a subset of the Carphodactylini — one that had perhaps already evolved padded toes independently — migrated into this marginal con-

tinental area, probably from the south. Here contact with the mainland near the Australo—Antarctic boundary was more extensive.

The subsequent opening of the Tasman Sea isolated the two divisions of the Carphodactylini and by 80 mybp the production of new sea floor between Australia and Tasmantis would have prevented interchange of most non-vagile animals. Spread of the two stocks probably proceeded rapidly. In Australia, the Late Cretaceous regression of epeiric seas was likely followed by westward expansion of the padless carphodactyline ancestors. In Tasmantis, carphodactylines had probably reached New Caledonia by the time of the Tasman rifting, and were certainly there by 65 mybp when the Lord Howe Rise sank and the New Caledonian Basin formed. Movement into New Guinea was blocked by the discontinuity in the Inner Melanesian Arc resulting from the formation of the Coral Sea. Interchange to parts of Northern New Zealand were probably possible as late as the Oligocene, at which time marine ingressions resulted in a large deep water gap along this portion of the Inner Melanesian Arc. The proximity of New Caledonia to Australia had ended with the formation of the Coral Sea as an extension of the Tasman, but contact was unlikely even before this.

In the Paleocene the initiation of movement along the Alpine Fault in New Zealand probably separated the variably emergent northern Australian Plate regions, with their connections to New Caledonia, from the southern Pacific Plate parts of New Zealand. The counter-clockwise rotation of the Pacific Plate caused subduction of its western margin under the Australian plate, resulting in the orogenic event that produced the Great Dividing Range in eastern Australia (53 mybp). These events isolated the ancestors of *Naultinus* and the southern species of *Hoplodactylus* from the northern *Hoplodactylus* and New Caledonian ancestors. In Australia, they divided the *Nephrurus* and *Phyllurus* + *Carphodactylus*.

In Australia during the Eocene, the opening of the Southern Ocean initiated the modern weather system patterns in the Southern Hemisphere. Members of both the Diplodactylini, probably long present in western Australia, and the padless carphodactylines moved with the continent into more northern latitudes, where desertification of much of the central and western parts of the continent occurred. The *"Underwoodisaurus" (Nephrurus milii* and *N. sphyrurus)* remained in association with coastal regions and with the western flanks of the Dividing Range, while the ancestors of the knob-tailed geckos evolved in the more xeric, sandy areas of the interior. *Nephrurus milii* has probably achieved its huge range only since the Late Miocene, when a coastal route around the western side of Australia would have been possible. Inland spread is probably still more recent and may have followed the drying of the lake systems. The isolated records of *N. milii* in Northern Territory, Australia may represent an introduction, or may be the result of a successful invasion via rocky corridors to the McDonnell Ranges.

Following the appearance of those characters shared by the knob-tailed group (Node 4), such as spinose subdigital scales and the knob itself, *Nephrurus* evolved into two lineages on either side of the central Australian continental lake system: a northern

lineage, resulting in *N. asper* in the Northern Territory and Queensland and *N. wheeleri* in Western Australia, and a southern lineage, the smooth knob-tails. Subsequent to the drying of the lake system since the Miocene, *Nephrurus* has invaded the entire arid region and has undergone species specific habitat specialization (Pianka 1972).

In eastern Australia the division of the *Phyllurus* and *Carphodactylus* lineages is obscure, but habitat barriers of savannah vegetation have existed in coastal Queensland at least since the Pleistocene (Kikkawa et al. 1981) and remnants of the continental lake system in northern Queensland may have been responsible for the division of these groups. Today *Carphodactylus* is found only in the region of the Atherton Tablelands. *Phyllurus* occurs from northern Queensland south to the sandstone area of the Sydney—Hawkesbury drainage. It is possible that a smaller, southern rupicolous form *(P. platurus)* and a larger, northern arboreal form *(P. cornutus)* have each given rise to a sister species with different habitat preferences. Separation of populations leading to speciation may have been a recent result of rising post-Pleistocene sea levels, and it continues as rainforest fragmentation separates populations of the arboreal forms, particularly *P. cornutus*.

Parts of Tasmania remained submerged for most of the early part of the Tertiary. If Tasmania was not colonized by geckos before the Early Miocene, when Australia moved into its present latitude, it is likely that colder Bassian climates and occasional ocean barriers would have prevented subsequent movement into this region. Thus, no geckos are present in Tasmania today.

In New Zealand, the initiation of movement along the Alpine Fault some 50 mybp isolated the two groups of padded carphodactyline geckos. Both groups primitively had the features of a pigmented mouth, tongue and peritoneum, ovoviviparity, and tail prehensility. In the Pacific Plate region (Torlesse terrane and others) of New Zealand, a prior (unknown) event was associated with the division of the ancestral *Naultinus* stock from the ancestral *Hoplodactylus* (sensu lato) that had probably spread northward prior to the opening of the Tasman. From the Paleocene through the Miocene, the two portions of New Zealand were variably emergent, but were not close.

Within the southern terranes, Oligocene ingressions probably greatly reduced the available land area. Not until the Pliocene Kaikoura Orogeny did the present rugged topography of the region appear. Associated with these movements, *Hoplodactylus granulatus* was probably isolated in the Kaikouras themselves, and eventually evolved into the modern sub-alpine species *H. kahutarae*. At the same time, or perhaps earlier, a similar event in the far south led to the eventual evolution of *Hoplodactylus rakiurae* on Stewart Island. Until the early Pleistocene, the ancestors of modern *Naultinus* remained in the South Island where they evolved diurnality, perhaps in association with the low temperatures of the region and the absence of predators and competitors. With the Kaikoura Orogeny and the Pleistocene glaciations, the range of *Naultinus* became fragmented, and this led to their present degree of differentiation. In the north geckos similar to *N. manukanus* invaded the North Island where they successfully established very recently. In the northern South Island, the retreat of the glaciers opened up corridors between formerly isolated populations that had become behaviorally, and

somewhat morphologically distinct. In some regions in Nelson, rather distinct forms occur in near sympatry.

Following their isolation from narrow-padded forms in the Paleocene, the ancestors of the broad-padded *Hoplodactylus* had spread northward into New Caledonia before the onset of peak Oligocene ingressions. Northland, which has a long emergent history, may have been the site of early divergence within the broad-padded *Hoplodactylus*. *Hoplodactylus pacificus* is currently limited to the North Island north of the line of an early Miocene seaway from Taranaki to Hawkes Bay. On the other hand, *H. maculatus* is distributed throughout New Zealand and, like *H. granulatus*, may have invaded the other island during the latest Tertiary or Quaternary. *Hoplodactylus chrysosireticus, H. stephensi* and probably *H. delcourti* have (or had) restricted ranges and at least the former two may be relatively recent derivatives of ancestors shared with *H. maculatus* or *H. pacificus. Hoplodactylus chrysosireticus* may have been isolated in Taranaki by the rising of Mt. Egmont (G.R. Stevens 1980b) subsequently arriving on Mana Island and in the northwest coastal islands via dispersal in the very recent past; alternatively, it may have once enjoyed a wider range, disrupted by the Taranaki vulcanism and the rising post-Pleistocene sea levels. The origin of *H. stephensi* is problematical, as is the origin of certain other Stephens Island endemics, but probably relatively recent.

Hoplodactylus duvaucelii once had a much wider range than it has today; it was widespread on the mainland in pre-human times (Worthy 1987). Today, along with the tuatara and the skinks *Cyclodina macgregori* and *C. whitakeri*, it is limited in its distribution to the northern offshore islands of New Zealand and the islands of Cook Strait. The extermination of these species on the mainland, and the extinction of *Hoplodactylus delcourti* is related to the simultaneous arrival of man and the kiore *(Rattus exulans)*. Large, nocturnal reptiles are particularly vulnerable to rats (Thomas 1982a; Whitaker 1973, 1978) and *H. duvaucelii*, for example, occurs on rat inhabited islands only in rocky cliff areas. Its present distribution on islands is also limited by island size and habitat diversity (Towns & Robb 1986; Towns et al. 1985).

The carphodactylines of New Caledonia may have arrived in that region even before the opening of the Tasman Sea, but certainly no later than the Oligocene. A time prior to the sinking of the Lord Howe Rise (65 mybp) seems likely. In many ways *Bavayia* resembles the smaller North Island species of *Hoplodactylus* except for the presence of divided subdigital scansors and a subcaudal scansorial pad. *Bavayia* also differs from the New Zealand species in that it is oviparous rather than viviparous. No vicariant event appears to account for the division of the species complexes of *Bavayia* in New Caledonia. Both groups probably invaded the Loyalty Islands in the Quaternary. It is possible that *B. sauvagii* was established first on Maré, which has risen the greatest amount and was the first of the islands to rise. A subsequent *B. cyclura/B. crassicollis* dispersal event (or events) may have resulted in the population of all three islands by this form. *Bavayia sauvagii* may be habitat-limited or may be unable to compete with its larger congeners in the simpler habitats of Lifou and Ouvéa.

Eurydactylodes and *Rhacodactylus* are among the most bizarre of living geckos. Both

genera are associated largely with regions of ultrabasic rocks resulting from the Eocene overthrusting of peridotite sheets (Dubois et al. 1973; Avias 1973). These rocks have greatly affected the evolution of the highly endemic flora of New Caledonia (Guillaumin 1921, 1964; Virot 1956; Schmid 1981; Morat et al. 1986; Jaffré et al. 1987). These two gekkonid genera may have evolved in the late Eocene or slightly later in association with the edaphic plants of the ultramafic formations and their associated arthropods.

Eurydactylodes occurs in association with scrub vegetation in areas of both high and low rainfall. *Rhacodactylus* is primarily found in very wet areas. Both genera occur in southern, central and northeastern New Caledonia. No records exist from the north-western parts of New Caledonia or from non-ultramafic areas, although there are in-dications that *R. leachianus* once occurred in the Belep Islands in the far north, but even these are covered in peridotite sheets. Distributions of individual species are discussed in the species accounts. *Rhacodactylus auriculatus* and *R. sarasinorum* are found only in association with the southern third of New Caledonia, the area of the largest single mass of ultrabasics in the territory. Most of the other species are found chiefly in the central region of the island or in coastal forest regions of the northeast.

The species of the subgenus *Pseudothecadactylus* are highly modified *Rhacodactylus* distributed in three isolated populations in northern Australia. If the phylogenetic and geological hypotheses are accepted, it is inconceivable that these species were in Australia before the opening of the Tasman Sea. Despite the low vagility of carphodac-tylines (Bauer 1989a), it appears necessary to evoke a dispersal event for the arrival of *Pseudothecadactylus* in Australia. The PAUP analysis suggested that these animals were most closely related to *R. trachyrhynchus* and *R. sarasinorum*, to which they bear some general resemblance. Cogger & Heatwole (1981) suggested that a tropical dispersal route linked northeastern Queensland with Arnhem Land along the Gulf of Carpen-taria or further north during a period of marine regression. They also indicated that additional corridors led to the Kimberleys in Western Australia and suggested that the distribution of *Pseudothecadactylus* and the *Carlia fusca* complex might be explained by such a series of pathways. Pleistocene sea level drops also exposed several large areas between Australia and New Caledonia, including the Queensland Plateau and the Chesterfield Reefs (Holloway 1979; Gibbons 1985). It is unclear, however, whether this route across the Coral Sea would account for the extremely limited range of *Rhacodac-tylus australis* in Queensland today. Although the minor differences between *R. lindneri* and *R. cavaticus* are consistent with Pleistocene divergence, the large morphological gaps between *R. australis* and the more western species are difficult to reconcile with a Pleistocene arrival in Australia. It seems most probable that the ancestor of *R. australis* arrived over water from New Caledonia sometime in the late Tertiary and that habitat restrictions limited it from passing into New Guinea, which would have been connected by land to Queensland at the same time. Evolution of the *Rhacodactylus lindneri-cavaticus* form must have occurred shortly thereafter. The subsequent division of these species may have occurred as a result of migration over an Arafura Land bridge during periods of glaciation, with subsequent independent evolution following marine

ingressions in the post-Pleistocene. However, Cracraft (1986) proposed climatic ecological factors as the likely cause of the separation of the avifauna of Arnhem Land and the Kimberley Plateau. He also suggested that the arid region at the head of the Gulf of Carpentaria may have served to divide the biotas of Arnhem Land and the Cape York Peninsula. Either interpretation is consistent with the congruent patterns of species-area relationships in these three regions.

The absence of carphodactylines elsewhere in the southwest Pacific seems related largely to the low vagility of the species. Norfolk island and Lord Howe Island, which have been emergent only since the late Tertiary, and would have had to be colonized over water therefore lack these geckos.

The corroboration of the phylogenetic hypothesis by geological data in no way "proves" that the phylogeny is correct (Arnold 1981), but is does support its robustness by independent evidence. Further resolution within *Hoplodactylus* and an ecological analysis of *Rhacodactylus* may allow a far more detailed comparison with paleogeography. It may also further strengthen and confirm or improve parts of the preceding scenario. Analysis by karyological and immunological methods would also provide an independent test of the phylogenetic hypothesis and perhaps suggest particular dates of divergence for comparison with supposed vicariant events. The discovery of fossil material from New Caledonia or New Zealand would also do much to bolster the scenario, but unfortunately only Pleistocene and recent material are currently available.

CARPHODACTYLINE SPECIES ACCOUNTS

The following accounts present diagnoses and complete synonymies for all genera and species of carphodactyline geckos. The nomenclature employed is consistent with the preceding phylogenetic analysis in that only convex (sensu Meacham & Duncan 1987) genera are recognized. Species epithets follow the spelling of the original descriptions.

All known published variants of names are included in the synonymies. Names appear more than once in a synonymy when an existing name, after a period of disuse, was employed again at a later date. Thus the synonymies reflect the complete history of the nomenclature of each taxon. Popular and semi-popular works are also included in some cases. For example, the works of Cogger (1975b, 1979, 1983, 1986) are the general references for the use of names of Australian reptiles and have as much, if not more, widespread influence than technical works dealing with the systematics of particular groups of taxa. Name changes proposed by Wells & Wellington (1984, 1985a, 1985b) are considered invalid and unsupported (see Thulborn 1986) and suppression of these works has been proposed (Anonymous 1987; Shea 1987). They are therefore excluded from the synonyms.

Keys are provided to the genera and species (see each generic account) of the Carphodactylini. A variety of keys is available for species of genera in the tribe. These include Roux (1913) and Sadlier (1989) for New Caledonian species, McCann (1955),

Towns (1985), and Gill (1986) for New Zealand species, and Cogger (1986), Storr (1963), and Covacevich (1975) for Australian carphodactylines. Boulenger (1885a) provided keys for the species known to him. Although exsting keys are sufficient for some genera (e.g. *Rhacodactylus*), many other keys require that determination be made from living specimens, adult males, original-tailed individuals or animals of known provenance; conditions that are not universally applicable. For this reason, new keys based on characters clearly visible on almost any museum specimen have been provided. In some circumstances the pre-existing keys should be consulted first since determination based on color or locality (if known) may be accomplished more rapidly. Members of the genus *Naultinus* as well as some *Nephrurus, Phyllurus* and *Hoplodactylus* may be particularly difficult to distinguish from one another.

A "Comments" section follows the synonymy and diagnosis of each species and genus. Because the biology of all carphodactylines is poorly known and the literature is scattered and often obscure, I present a summary of all known aspects of the biology of each taxon. All major references to size, distribution, taxonomy, ecology, behavior and reproduction are cited in these "Comments" sections. Unpublished accounts of the biology of some New Caledonian taxa gathered during this study are also included. Plotted distributions based on specimens examined and literature records are provided.

Key to the genera of carphodactyline geckos

1a. Subdigital scansorial lamellae absent 2
b. Subdigital scansorial lamellae present 4
2a. Middorsal row of enlarged body scales, body compressed ..... *Carphodactylus*
b. No enlarged middorsal scale row, body depressed 3
3a. Enlarged extra-brillar fringe, digits not kinked .... *Nephrurus*
b. Extra-brillar fringes not enlarged, digits kinked .... *Phyllurus*
4a. Lamellae divided 5
b. Lamellae undivided 6
5a. Digit I of manus clawless .... *Rhacodactylus (Pseudothecadactylus)*
b. All digits clawed .... *Bavayia*
6a. Penultimate phalanx of some digits partially subsumed in pad 7
b. Penultimate phalanx of all digits free of pad 8
7a. Body scales greatly enlarged, body compressed .... *Eurydactylodes*
b. Body scales small and granular or tubercular, body depressed ... *Rhacodactylus*
8a. Dorsal scales of snout and body subequal, pupil margins crenelated *Hoplodactylus*
b. Dorsal scales of snout enlarged, pupil margins smooth .... *Naultinus*

Bavayia **Roux, 1913**

1913 *Bavayia* Roux. Nova Caledonia, Zoologie, I(II): 85.

Type species: *Peripia cyclura* Günther, 1872 by original designation.

1954 *Bavaya* Underwood. Proc.Zool.Soc.London 124: 471 (lapsus pro *Bavayia* Roux, 1913).

1983 *Bavaia* Rösler. Salamandra 19: 223 (ex errore pro *Bavayia* Roux, 1913).

S p e c i e s   r e f e r r e d : *Bavayia crassicollis* Roux, 1913, *B. cyclura* (Günther, 1872), *B. montana* Roux, 1913, *B. ornata* Roux, 1913, *B. sauvagii* (Boulenger, 1883), *B. septuiclavis* Sadlier, 1989, *B. validiclavis* Sadlier, 1989.

D i a g n o s i s : A monophyletic genus diagnosed by the following characters: second epibranchial long and recurved, nearly contacting ceratobranchial; coracoid process of interclavicle posteriorly placed; digits scansorial, broadly dilated; scansors divided; assymmetrical terminal scansors on digit one; first infralabials (sometimes) contact behind mental; webbing between digits II-III-IV; tail relatively short, sub-cylindrical with subcaudal scansors (**15**, 20*, 39, 74, 80).

C o m m e n t s : Because of the superficial resemblance of these geckos to certain gekkonine genera, the special status of this endemic New Caledonian group was not recognized until Roux's (1913) review of the New Caledonian herpetofauna. Roux (1913) recognized a number of subspecies but these do not correspond exactly to the distinct (species level) populations now recognized (Sadlier 1989). In this paper *Bavayia* was reduced to two species complexes in the phylogenetic analysis, *B. sauvagii* (also incorporating *B. ornata*), *B. cyclura* (incorporating the remaining taxa). The key provided by Roux (1913) is sufficient to differentiate the two species complexes. Sadlier (1989) provides a key to species. A thorough revision of the genus is needed. *Bavayia* occurs throughout New Caledonia and the Loyalty Islands. It is probable that the Belep Isles and other smaller islands also support one or more species. These are by far the most widely distributed and ecologically generalized of the New Caledonian geckos. Forest habitats in New Caledonia represent one of the only cases in which co-occurring diplodactylines (*Bavayia* spp.) occur in greater density than sympatric gekkonines *(Nactus pelagicus)* to a significant degree. Typically throughout Australia the gekkonines *Heteronota binoei, Phyllodactylus (= Christinus) marmoratus* and *Gehyra* spp. rival or outnumber diplodactyline species.

Key to the Species of *Bavayia*

1a. Claw of thumb situated between the halves of cleft terminal scansor 2
b. Claw of thumb situated medial to a single terminal scansor 6
2a. Dorsal pattern with pale, broad vertebral stripe 3
b. Dorsal pattern composed of pale, transversely oriented blotches 4
3a. Preanal pores in two rows; supranasals generally separated by a single internasal
scale .... *B. validiclavis*
b. Preanal pores in a single row; internasal region fragmented ...... *B. septuiclavis*
4a. First pair of infralabials usually contacting medially .... *B. montana*
b. First pair of infralabials usually separated 5
5a. Distinct, bold, dark transverse bands bordering pale dorsal blotches . *B. cyclura*
b. Pale, dorsal blotches and dark bands obscure and poorly defined . *B. crassicollis*
6a. Lateral surface of hindlimb with distinct, contrasting pale spots on a dark
background .... *B. ornata*
b. Lateral surface of hindlimb without pale spots, or spots indistinct .. *B. sauvagii*

Bavayia crassicollis **Roux, 1913**

1913 *Bavayia cyclura crassicollis* Roux. Nova Caledonia, Zoologie I(II): 89.
Type locality: (hoc loco restricta — Kramer 1979) Maré, Iles Loyalty.
Lectotype: NMBA 6931 (designated by Kramer 1979).
1954 *Bavayia cyclura crassicollis* Underwood. Proc.Zool.Soc. London 124: 477.
1989 *Bavayia crassicollis* Sadlier. Rec.Aust.Mus. 40: 366.

D i a g n o s i s : Terminal scansor of digit I cleft; first infralabials generally separated
from one another; more than one row of preanal pores in males, fewer than 20 pores
in anterior row; pygal region of tail abruptly decreases in diameter at post-pygal border;
dorsum with poorly defined blotches, no vertebral stripe; venter often yellowish in life.

C o m m e n t s : *Bavayia crassicollis* was first described as a subspecies of *B. cyclura* by
Roux (1913) who considered it restricted to the Loyalty Islands. The species as presently
conceived (Sadlier 1989) occurs both in the Loyalties and the New Caledonian
mainland. It has also been taken of several smaller offshore islands, including the Ilot
de Hienghéne, a tiny coralline satellite.

In most respects the biology of *B. crassicollis* appears to be similar to that of *B. cyclura*,
although the former is somewhat larger (maximum 86 mm SVL — AMS R78349). The
species has been found in association with dead trees, bark and mangrove vegetation.
It occupies one of the widest ranges of any *Bavayia* species and seems to have a broad
tolerance of habitat types.

Bavayia cyclura **(Günther, 1872) (Fig. 21)**

1869 *Platydactylus pacificus* Bavay. Mém.Soc.Linn.Normandie 15: 8 (nec Gray, 1842).

1872 *Peripia cyclura* Günther. Ann.Mag.Nat.Hist. (4)10: 422.

Type locality: New Caledonia.

Syntypes: BMNH 71.4.16.30 (A—B), 71.4.16.31 (A—C). (71.4.16.31 (A—C) are *B. sauvagii*).

1873 *Lepidodactylus neocaledonicus* Bocage. J.Sci.Mat.Phys.Nat. Lisboa 4: 206.

Type locality: Nouvelle Calédonie.

Syntypes: MLI (specimen number unknown) destroyed by fire.

1878 *Hemidactylus (Peripia) bavayi* Sauvage. Bull.Soc.Philomat., Paris (7)3: 71.

Type locality: Nouvelle-Calédonie.

Syntypes: MNHN 5311-2. (5312 is a *B. sauvagii*).

1883 *Lepidodactylus cyclurus* Boulenger. Proc.Zool.Soc. London 1883: 121; pl. XXII (fig. 4).

1913 *Bavayia cyclura* Roux. Nova Caledonia, Zoologie I(II): 88.

1932 *Bavayia cyclura cyclura* Burt & Burt. Bull.Amer.Mus.Nat.Hist. 63: 497.

1965 *Bavayia cyclura* Wermuth. Das Tierreich 80: 9.

D i a g n o s i s : Terminal scansor of digit I cleft; first infralabials generally separated from one another; preanal pores of males in more than one row, fewer than 20 pores in anterior row; pygal region of tail abruptly decreases in diameter at post-pygal border; dorsum generally without vertebral stripe; venter yellowish in life.

Fig.21: a. Syntype of *Peripia cyclura* Günther, 1872 (= *Bavayia cyclura*). BMNH 71.4.16.30B. b. Syntype of *Hemidactylus (Peripia) bavayi* Sauvage, 1878 (= *Bavayia cyclura*). MNHN 5312. This specimen is referable to *Bavayia sauvagii*. c. Holotype of *Lepidodactylus sauvagii* Boulenger, 1883 (= *Bavayia sauvagii*). MNHN 5790. Although the type description matches the species associated with this name, the holotype is referable to the species now regarded as *Bavayia cyclura*. (Photos courtesy of Ross Sadlier, The Australian Museum)

Comments: *Bavayia cyclura* was first noted by Bavay (1869) as *Platydactylus pacificus*. Günther's (1872) description is inadequate to differentiate *cyclura* from other species and probably inadequate to identify the genus. The species is known from all areas of New Caledonia as well as the three Loyalty Islands and the Isle of Pines (Fig. 22). (Pending a thorough review of the *B. cyclura* complex *(B. crassicollis, B. cyclura, B. montana, B. septuiclavis)* no distinction between taxa is made on the distribution map).

Bavay (1869) found the species common throughout New Caledonia except in association with houses. He stated that 15—20 could be found under bark associated with small grey scorpions. Roux (1913) stated that *B. cyclura* could be found under bark or in rotten wood. I have collected this species in houses and under debris (rarely) and in rotten trees and stumps as well as under bark. The species is more common than most of its congeners in drier parts of the island, e.g. the west coast and at middle elevations. In natural situations it is almost invariably associated with dead wood. These geckos apparently spend daylight hours under bark and emerge after sunset to forage on the ground and on tree trunks. This species is of moderate size, the largest specimen
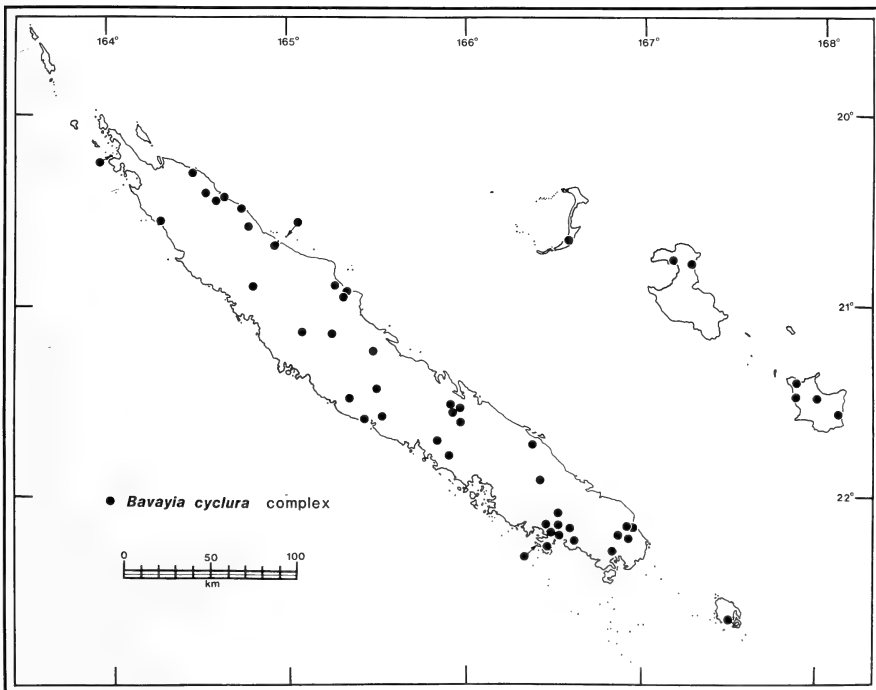

Fig.22: Distribution of the *Bavayia cyclura* complex in New Caledonia and the Loyalty Islands.

reaching 72 mm SVL (Bauer & Vindum, in press). Natural diet appears to consist chiefly of arthropods (Bauer & DeVaney 1987). Members of the *B. cyclura* complex display greater aggressive behavior than those of the *sauvagii* group and frequently bite when captured. The two eggs are relatively large and breeding apparently takes place, at least in the range as a whole, all year. This species may be found in association with *Rhacodactylus* in tree holes (Meier 1979). Russell (1972, 1979a) has examined the foot morphology of members of the *B. cyclura* complex.

Bavayia montana Roux, 1913

1913 *Bavayia cyclura montana* Roux. Nova Caledonia, Zoologie I(II): 88.
Type locality: (hoc loco restricta — Kramer 1979) Mount Ignambi, 700-800 m, Nouvelle-Calédonie.
Lectotype: NMBA 6954 (designated by Kramer 1979).
1989 *Bavayia montana*. Sadlier. Rec.Aust.Mus. 40: 366.

D i a g n o s i s : Terminal scansor of digit I cleft; first infralabials generally contact one another medially; preanal pores in males in more than one row, typically 20 or more pores in anterior row; pygal region of tail abruptly decreases in diameter at post-pygal border; dorsum generally dark with transverse blotches, no vertebral stripe; venter yellowish in life.

C o m m e n t s : *Bavayia montana* is restricted to the mountains of the east coast chain of New Caledonia (Roux 1913). This species is relatively large (maximum 76 mm SVL — NMBA 6942) and thick bodied. It prefers more mesic environments than most of its congeners and has been found in tree fern fronds and on *Pandanus* (Roux 1913) as well as under moist rotten logs and within rotted tree stumps. Although it occurs at elevations of up to 930 m, it has also been collected at 80 m on Mt. Koyaboa, near Poindimié, just upslope from *B. sauvagii*.

Bavayia ornata Roux, 1913

1913 *Bavayia sauvagei ornata* Roux. Nova Caledonia, Zoologie I(II): 92; pl. IV (fig. 3).
Type locality: Forêt du Mont Panié, altit. 500 m, Nouvelle-Calédonie.
Lectotype: NMBA 7025 (designated by Kramer 1979).
1989 *Bavayia ornata*. Sadlier. Rec.Aust.Mus. 40: 366.

D i a g n o s i s : Terminal scansor of digit single, medial; cloacal spurs in males rounded; pygal region of tail tapers into post-pygal; preanal pores in male, in a single transverse row; lateral surface of hindlimbs with distinct pale spots; venter whitish in life. (75, **102**).

C o m m e n t s : This species appears to be restricted in distribution to the lower slopes of Mt. Panié in northeastern New Caledonia (Fig. 23). This relatively small (maximum 69 mm SVL — NMBA 7023) species is extremely gracile and is found in closed forest (Sadlier 1989) beneath bark or in rotten stumps. Nothing is known of the biology of *B. ornata*.

Bavayia sauvagii (Boulenger, 1883) (Fig. 21)

1878 *Hemidactylus cyclura* Sauvage. Bull.Soc.Philomat., Paris (7)3: 72 (nec Günther, 1872).

1883 *Lepidodactylus sauvagii* Boulenger. Proc.Zool.Soc. London 1883: 122; pl. XXII (figs. 5,5a).

Type locality: New Caledonia.

Holotype: MNHN 5790. (The type description is clearly that of the species now recognized as *Bavayia sauvagii*, however, the specimen now labeled as the holotype itself is conspecific with *B. cyclura*).

1913 *Bavayia sauvagei* Roux. Nova Caledonia, Zoologie I(II): 91; pl. IV (figs. 2,2a) (nomen emendatum pro *Bavayia sauvagii* Boulenger, 1883).

1932 *Bavayia sauvagii sauvagii* Burt & Burt. Bull.Amer.Mus.Nat.Hist. 63: 497.

1954 *Bavaya sauvagei* Underwood. Proc.Zool.Soc. London 124: 477.

1965 *Bavayia sauvagii* Wermuth. Das Tierreich 80: 9.

D i a g n o s i s : Terminal scansor of digit I single, medial; cloacal spurs in males somewhat pointed; pygal region of tail tapers into post-pygal; preanal pores in a single transverse row; lateral surface of hindlimbs without distinct pale spots; venter whitish in life. (75, **102**).
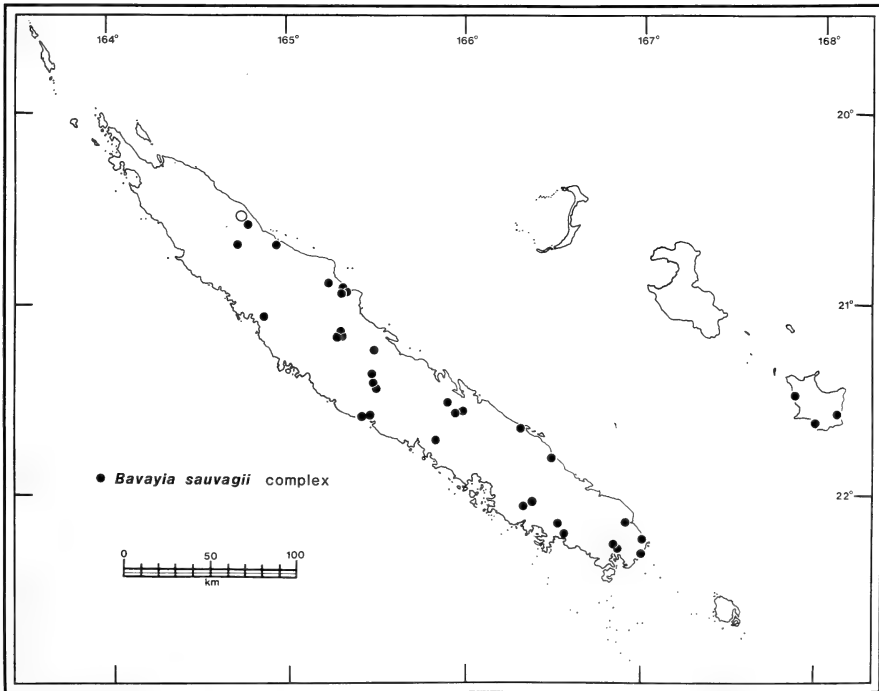

Fig.23: Distribution of the *Bavayia sauvagii* complex in New Caledonia and the Loyalty Islands. *B. sauvagii* (closed circles), *B. ornata* (open circles).

C o m m e n t s : This species was not initially recognized as being distinct from *Bavayia cyclura*. Perhaps because of the partial division of some distal scansors, Sauvage (1878) placed this form in the genus *Hemidactylus*, although he believed that he was examining *B. cyclura*. The range of the species as a whole encompasses the whole of the mainland (except for the far north), and Maré (Fig. 23). It is likely that this species is also present on the Isle of Pines and perhaps on the other Loyalty Islands and in northern New Caledonia. Alternatively, the species may be restricted in its distribution by low rainfall and unsuitable cover in the aforementioned areas.

Roux found *B. sauvagii* under rocks and logs in forested areas. I have collected it primarily under rocks by day in areas of high to very high rainfall (Bauer & DeVaney 1987) (Fig. 24). At night these geckos may be found climbing on the trunks of saplings and smaller trees. *Bavayia sauvagii* appears to be partially active under stones all day, although peak activity is several hours after sunset. At Poindimié this small species (maximum 62 mm SVL — CAS 162184) may be found in association with a variety of terrestrial lizards — *Nactus pelagicus, Marmorosphax tricolor, Nannoscincus mariae, N. gracilis* as well as with scorpions and large millipedes. Two or three individuals may be found under a single stone. These animals frequently occupy crevices in loose rock banks. At Mt. Koyaboa this species occurs only at lower elevations (<50 m). *Bavayia*

Fig.24: Typical secondary forest habitat of *Bavayia sauvagii* at low elevation on Mt. Koyaboa, Poindimié, New Caledonia.

montana is found in low numbers above 80 m on the same slopes. Like *B. cyclura*, this species apparently breeds all year long. The diet is varied and consists chiefly of arthropods, particularly crickets and isopods. Ants, though very abundant are only rarely taken (Bauer & DeVaney 1987). Remains of *Bavayia sauvagii* have been found in the stomach of *Rhacodactylus auriculatus*.

Bavayia septuiclavis Sadlier, 1989

1989 *Bavayia septuiclavis* Sadlier. Rec.Aust.Mus. 40: 367.
Type locality: 4 km along Mt. Gouemba road from turnoff on Yate-Goro road (300—350 m), 22°09'S x 166°54'E, New Caledonia.
Holotype: AMS R78139.

D i a g n o s i s : Terminal scansor of digit I cleft; scales of internasal region fragmented; infralabials generally separated from one another; preanal pores in males in a single row; pygal region of tail abruptly decreases in diameter at post-pygal border, tail slender; dorsum with a broad, light colored vertebral stripe.

C o m m e n t s : *Bavayia septuiclavis* is known from only two localities in southern New Caledonia. It has similar habitat preferences to *B. sauvagii* and has been found sheltering under stones by day and active on tree trunks and branches by night (Sadlier 1989), Maximum 50 mm SVL (Sadlier 1989).

Bavayia validiclavis Sadlier, 1989

1989 *Bavayia validiclavis* Sadlier. Rec.Aust.Mus. 40: 367.
Type locality: Mt. Panie (500—600 m), 20°33'S x 164°45'E, New Caledonia.
Holotype: AMS R77855.

D i a g n o s i s : Terminal scansor of digit I cleft; supranasal scales generally separated by a single internasal; first infralabials generally separated from one another; preanal pores in males in more than one row; pygal region of tail abruptly decreased in diameter at post-pygal border; dorsum with a broad, light colored vertebral stripe.

C o m m e n t s : *Bavayia validiclavis* is restricted to the northeastern mountains of mainland New Caledonia. This is the smallest species of the genus and the smallest carphodactyline with a maximum SVL of 45 mm (Sadlier 1989). Little is known of its biology but it appears to be similar to *B. sauvagii* and *B. septuiclavis* (Sadlier 1989).

Carphodactylus Günther, 1897

1897 *Carphodactylus* Günther. Novit.Zool. 4: 403.
Type species: *Carphodactylus laevis* Günther, 1897 by monotypy.
S p e c i e s   r e f e r r e d : *Carphodactylus laevis* Günther, 1897.
D i a g n o s i s : A monotypic taxon diagnosed by the following characters: Trunk vertebrae somewhat procoelous; two ribless cervical vertebrae; neural spines of trunk high — giving the body a compressed appearance; first autotomy septum in fifth caudal

vertebra; coracoid process of interclavicle indistinct; anterior loreal scales minute; mid-dorsal scales enlarged to form a low crest; preanal organs present but weakly developed; tail elongate, compressed, without spinose scales, terminating in a tiny knob; cloacal spurs bear a darkly pigmented spot; toes bear non-scansorial lamellae; extra-brillar fringes prominent; canthus prominent. (15, 48*, 58*, **68**, 97*).

C o m m e n t s : This little-known monotypic genus was the last of the carphodactyline genera to be discovered. Kluge's (1967b) choice of the tribal name Carphodactylini derives from his belief that this genus exhibited the greatest number of primitive traits.

Carphodactylus laevis **Günther, 1897 (Fig. 25)**

1897 *Carphodactylus laevis* Günther. Novit.Zool. 4: 403, pl.XI.
Type locality: Mt. Bartle Frere, Queensland.
Holotype: presumed lost (fide Cogger et al. 1983).

D i a g n o s i s : As for genus.

C o m m e n t s : Günther's (1897) description of *Carphodactylus laevis* is adequate and appears to describe an individual with a regenerated tail, since no mention of the caudal knob characteristic of original tails is made. Cogger (1986) reported a maximum SVL of 130 mm. The species is distributed within the area 15°49'—17°23'S by 145°17'—145°49'E, a small patch of coastal mountainous terrain running from about Tully north to Cooktown, Queensland (Fig. 26). This southern Cape York endemic occurs in rainforest areas and has been claimed to be both arboreal (Worrell 1963) and terrestrial (Loveridge 1934), although an intermediate ecology appears most likely (Cogger 1983; Wilson & Knowles 1988). *Carphodactylus laevis* is primarily insectivorous. This is the only Australian carphodactyline proposed for international protection (Ehmann & Cogger 1985), and Czechura & Covacevich (1985) considered it to be at indeterminate risk due to its patchy distribution within the range.

Fig.25: *Carphodactylus laevis* Günther, 1897 AMS R10838. SVL = 92 mm. (Scientific Photography Laboratory, U.C. Berkeley)
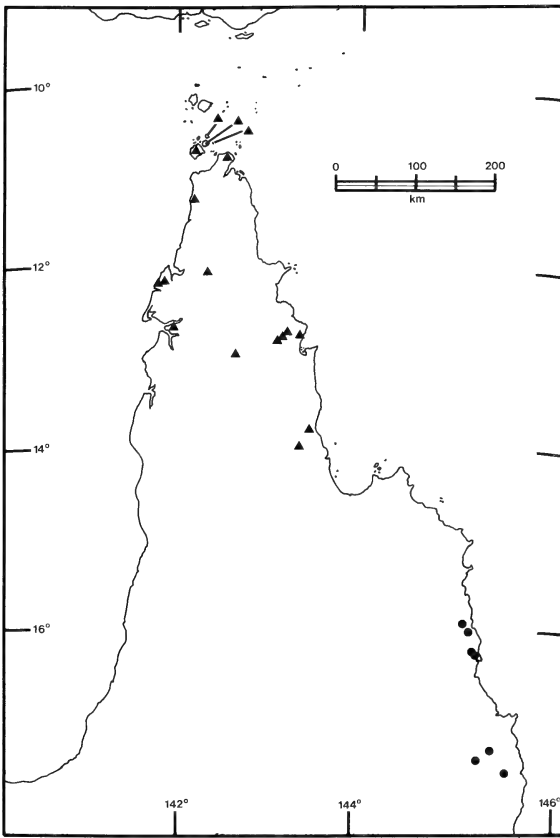
Fig.26: Distribution of *Rhaco-dactylus australis* (triangles) and *Carphodactylus laevis* (circles) in northern Queensland.

Eurydactylodes **Wermuth, 1965**

1878 *Eurydactylus* Sauvage. Bull.Soc.Philomat., Paris (7)3: 70 (non *Eurydactylus* Laferte, 1851 = Coleoptera; non *Eurydactylus* Hagedorn, 1909 = Coleoptera).
Type species: *Platydactylus vieillardi* Bavay, 1869 by monotypy.
1883 *Eurydectylus* Boulenger. Proc.Zool.Soc. London 1883: 129. (error typographicus (in synonymy) pro *Eurydactylus* Sauvage, 1878).
1965 *Eurydactylodes* Wermuth. Das Tierreich 80: IX (nomen novum pro *Eurydactylus* Sauvage, 1878).

S p e c i e s   r e f e r r e d : *Eurydactylodes symmetricus* (Andersson, 1908); *E. vieillardi* (Bavay, 1869).

D i a g n o s i s : (Node 17) A monophyletic taxon diagnosed by the following characters: Fewer than 30 scleral ossicles; neural spines of trunk vertebrae very high,

giving body a compressed appearance; six or seven inscriptional ribs; dorsal body scala-
tion heterogeneous, consisting of enlarged, smooth, flat scales; claw lies between two
separate terminal scansors*; folds of loose skin on posterior face of hind limb; tail with
subcaudal lamellae and ventral sulcus; slit from angle of mouth to ear*; endolymphatic
sacs expanded extra-cranially*. (15, 22, 32-C, **74**, 90, **102**, 104, 105).

C o m m e n t s : This small genus is among the least well known of the carphodactyline
groups. Underwood (1954) initially placed this genus in the Gekkoninae but later (1955)
moved it to the Diplodactylinae. *Eurydactylodes* is limited in its distribution to the
main island of New Caledonia and appears to be fairly widely distributed except on the
dry west coast of the island (Fig. 27). Both species may be locally abundant; the few
specimens in collections probably reflect the difficulty in spotting these small cryptic
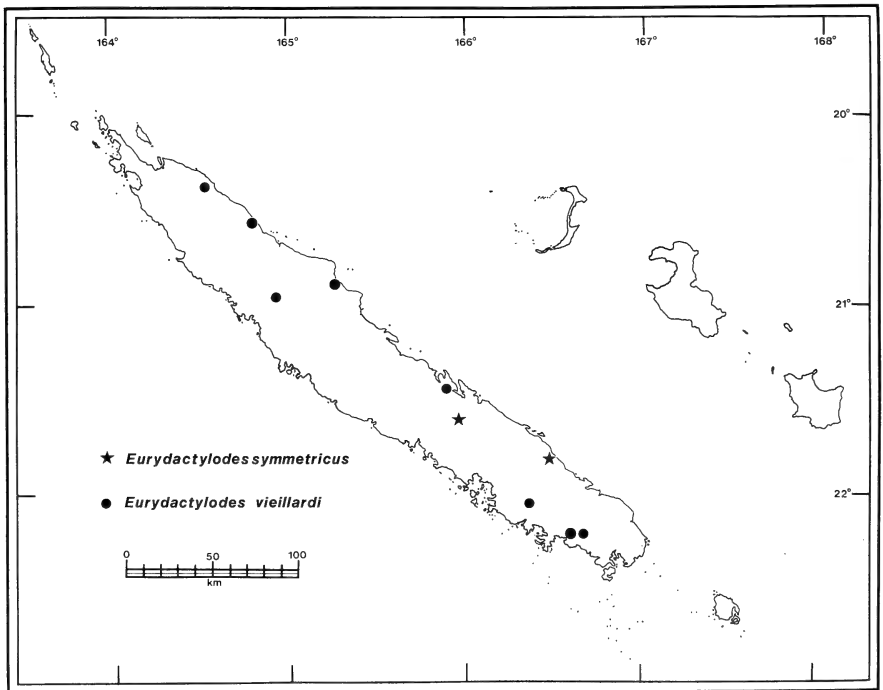geckos.

Fig.27: Distribution of *Eurydactylodes symmetricus* (stars) and *E. vieillardi* (circles) in New
Caledonia.

Key to the Species of *Eurydactylodes*

1a. Cruciform patch of raised, rounded scales on nape. Dorsal head scales enlarged, regularly arranged and generally in contact .... *E. symmetricus*
b. No raised scales on nape. Enlarged dorsal head scales usually irregularly arranged, separated by smaller interscales .... *E. vieillardi*

Eurydactylodes symmetricus (Andersson, 1908) (Fig. 28)

1908 *Eurydactylus symmetricus* Andersson. Ark.Zool. 4(14): 1, fig. 1a-1d.
Type locality: New Caledonia.
Holotype: NHMG 651.
1965 *Eurydactylodes symmetricus* Wermuth. Das Tierreich 80: 30.

D i a g n o s i s : Nape with cruciform patch of raised tubercles; head scales generally large; symmetrical without small interscales; slit from mouth to ear continuous.

C o m m e n t s : Andersson's (1908) description is detailed, as is his re-diagnosis of the genus. However, the characters proposed by Andersson (1908) and Roux (1913) to separate this species from *E. vieillardi* are too variable to be reliable.

Fig.28: Holotype of *Eurydactylus symmetricus* Anderson, 1980 (= *Eurydactylodes symmetricus*). NHMG 651. Total length = 93 mm. (Photo courtesy of Ross Sadlier, The Australian Museum)

Eurydactylodes symmetricus reaches a SVL of 69 mm (Andersson 1908) and has been collected in forest at 200 m (Roux 1913) and 510 m altitude (MNHN 1985-123). Nothing is known of its biology.

Eurydactylodes vieillardi (Bavay, 1869) (Fig. 29)

1869 *Platydactylus vieillardi* Bavay. Mém.Soc.Linn. Normandie 15: 10.
Type locality: Canala, Neu Kaledonien. (Type locality of Bavay (1869) = Houagape (= Wagap), Nouvelle-Calédonie).
Holotype: EMNB (specimen number unknown), presumed lost.
Neotype: ZFMK 46981, here designated.
1878 *Eurydactylus vieillardi* Sauvage. Bull.Soc.Philomat., Paris (7)3: 70 (lapsus pro *Platydactylus vieillardi* Bavay, 1869).
1883 *Eurydectylus vieillardi* Boulenger. Proc.Zool.Soc. London 1883: 129; pl. XXII (figs. 7,7a,7b) (error typographicus).
1885 *Eurydactylus vieillardi* Boulenger. Catalogue of Lizards in the British Museum vol.1: 192.
1932 *Eurydactylus vieillardi* Burt & Burt. Bull.Amer.Mus.Nat.Hist. 63: 479.
1934 *Eurydactylus vieillardi* Brongersma. Zool.Meded. 17: 166.
1965 *Eurydactylodes vieillardi* Wermuth. Das Tierreich 80: 30.

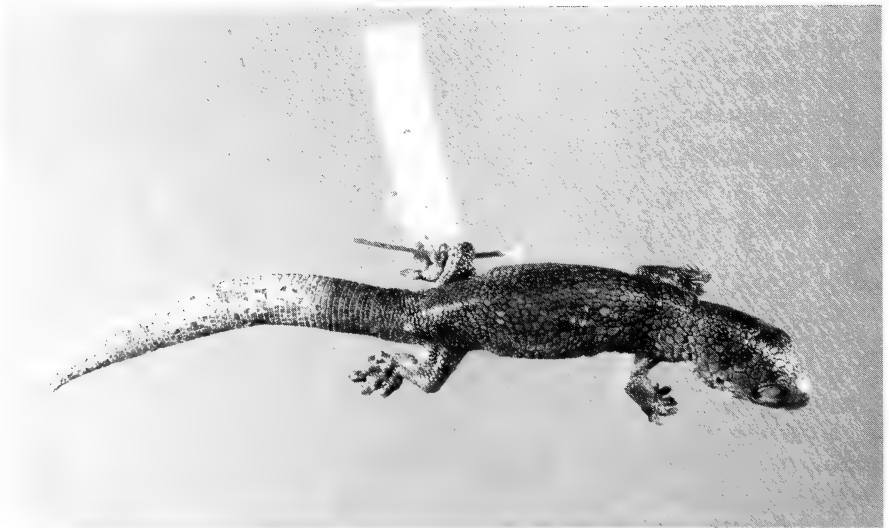Fig.29: Neotype of *Eurydactylodes vieillardi* (Bavay, 1869). ZFMK 46981. (Photo courtesy of J. Schicke, Zoologisches Forschungsinstitut und Museum A. Koenig)

Fig.30: Carénage River, southern ultramafic region of New Caledonia. Typical peridotite habitat of *Eurydactylodes vieillardi* and *Rhacodactylus auriculatus*.

D i a g n o s i s : Scales of nape similar those of dorsum; head scales irregular, separated by small interscales; slit from mouth to ear interrupted anterior to meatus.

C o m m e n t s : The description of *Eurydactylodes vieillardi* (Bavay, 1869) is complete and sufficient to diagnose the genus.

Like its congener, this species is widely distributed in central and eastern New Caledonia (Figs. 27,30). It has been collected from the branches of bushes (Roux 1913; Meier 1979). Sauvage (1878) describes the eggs of this species, which appear to be among the largest in the family in relative size. Maximum adult SVL is 57 mm (MNHN 699-1863).

Hoplodactylus Fitzinger, 1843

1842 *Naultinus* (part) Gray. Zool.Misc.: 58.
Type species: *Naultinus pacificus* Gray, 1842 by original designation.
1843 *Hoplodactylus* Fitzinger. Systema Reptilium: 100 (non *Hoplodactylus* Agassiz,

1845 = Echinodermata; non *Hoplodactylus* Chaudoir, 1878 = Coleoptera).

Type species: *Platydactylus duvaucelii* Duméril & Bibron, 1836 by original designation.

1845 *Pentadactylus* Gray. Catalogue of the Specimens of Lizards in the British Museum: 160.

Type species: *Platydactylus duvaucelii* Duméril & Bibron, 1836 by monotypy.

1867 *Dactylocnemis* Steindachner. Reptilien. Reise der Fregatte Novara: 11.

Type species: *Naultinus pacificus* Gray, 1842 by monotypy.

1901 *Woodworthia* Garman. Bull.Mus.Comp.Zool. 39: 4.

Type species: *Woodworthia digitata* Garman, 1901 by monotypy.

1913 *Woodwarthia* Roux. Nova Caledonia, Zoologie I(II): 86 (lapsus pro *Woodworthia* Garman, 1901).

S p e c i e s   r e f e r r e d : *Hoplodactylus chrysosireticus* Robb, 1980; *H. delcourti* Bauer & Russell, 1986; *H. duvaucelii* (Duméril & Bibron, 1836); *H. granulatus* (Gray, 1845); *H. kahutarae* Whitaker, 1985; *H. maculatus* (Gray, 1845); *H. pacificus* (Gray, 1842); *H. rakiurae* Thomas, 1981; *H. stephensi* Robb, 1980.

D i a g n o s i s : This is a paraphyletic group and as such cannot be diagnosed. The species included in *Hoplodactylus* are those which share the characters present at Node 11 but none of those present at or above Node 14 (Fig. 18).

C o m m e n t s : The history of the genus *Hoplodactylus* is intimately interwoven with that of *Naultinus*. The genus was erected by Fitzinger (1843) to accomodate *Platydactylus duvaucelii* Duméril & Bibron, 1836. Instability at the generic level has occurred in several instances. Steindachner (1867) erected *Dactylocnemis* to accommodate Gray's (non-diurnal) *Naultinus*, believing these forms to be substantially distinct from *Hoplodactylus duvaucelii*, at that time believed confined to Bengal. Garman (1901), apparently lacking comparative *Hoplodactylus* material, introduced another genus, *Woodworthia*. Smith (1933a) settled the generic synonymies which are accepted here, although Chrapliwy et al. (1961) detected the historical error in the application of the names *Hoplodactylus* and *Naultinus* and proposed the use of *Naultinus* solely for the New Zealand "brown" geckos. Myers (1961) successfully argued for the retention of the names as currently used.

There are nine species in the genus, many of which have been only recently described. These geckos are typically terrestrial or saxicolous, although some, especially *H. granulatus*, may be more arboreal. The genus is distributed throughout New Zealand and its offshore islands (Pickard & Towns 1988). It includes the most southerly gecko in the world, *H. rakiurae* (Thomas 1981) and the largest gecko in the world, *H. delcourti* (Bauer & Russell 1986). All species are ovoviviparous and typically give birth to two young at a time. Although primarily insectivorous, several species are known to eat fruits and seeds (Whitaker 1968, 1982, 1987; Barwick 1982). A number of detailed ecological studies have been performed on species of *Hoplodactylus* (Whitaker 1968, 1982; Barwick 1982). Hardy (1972) and Allison (1982) reviewed the extensive literature on the parasites of the genus. Millener (1981) recorded the presence of fossils from a number of sites in New Zealand, some of which have since been referred to *Hoplodactylus* (Worthy 1987).

Key to the Species of *Hoplodactylus*

1a. Apical terminal scansors absent or present on all digits 2
b. Apical terminal scansors on digit I only 3
2a. No apical scansors on digits (gray with faint transverse bars — Seaward Kaikouras)
.... *H. kahutarae*
b. Apical scansors on all digits (harlequin pattern — Stewart Island) .. *H. rakiurae*
3a. Rostral contacts nostril 4
b. Rostral excluded from nostril by anterior nasal 8
4a. Proximal portion of toe two or more times width of distal portion, penultimate
phalanx strongly arched, clearly arising from within expanded pad 5
b. Proximal portion of toe less than twice width of distal portion 6
5a. 25 or more lamellae under fourth toe (longitudinally striped pattern — unknown
locality) .... *H. delcourti*
b. 20 or fewer lamellae under fourth toe (pattern of transverse chevrons, invariably
with light markings on nape — offshore islands of the North Island and Cook Strait)
.... *H. duvaucelii*
6a. Penultimate phalanx does not arise from within pad (pattern variable, invariably
with a white mark between eye and ear) .... *H. granulatus*
b. Penultimate phalanx arises from within pad 7
7a*. Approx. 7 scale rows on free portion of digit IV of pes, 6—9 rows of preanal pores
in males .... *H. stephensi*
b. Approx. 12 scale rows on free portion of digit IV of pes, 1—4 rows of preanal pores
in males .... *H. pacificus*
8a.** Rostral 2 times broader than deep .... *H. maculatus*
b. Rostral 2.5—3 times broader than deep .... *H. chrysosireticus*

* Striped specimens of *H. pacificus* are extremely difficult to distinguish from *H. stephensi*.
Because the ranges of these two species are non-overlapping, locality, if known, should be ac-
cepted as supplemental evidence of identity.

** This species pair is even more difficult to distinguish than the previous as ranges overlap. Robb's
(1980b) color description may be the only way to distinguish *H. chrysosireticus* from striped *H.
maculatus* with certainty. I have seen too few specimens of the former animal to judge the validity
of her pattern criteria.

Hoplodactylus chrysosireticus **Robb, 1980 (Fig. 31)**

1980 *Hoplodactylus chrysosireticus* Robb. New Zealand Amphibians and Reptiles in
Colour: 57; pl. 12 (upper left and middle).
1980 *Hoplodactylus chrysosireticus* Robb. Rec.Natl.Mus. New Zealand 1: 306; fig. 1A.
Type locality: Taranaki, North Island, New Zealand).
Holotype: NMNZ R25.

D i a g n o s i s : Digits broadly expanded, bearing scansors; terminal scansors present
on digit one only; rostral excluded from nostril; rostral 2.5-3.0 times broader than deep;
tail prehensile; mouth and tongue not distinctly pigmented; peritoneum black; dorsum
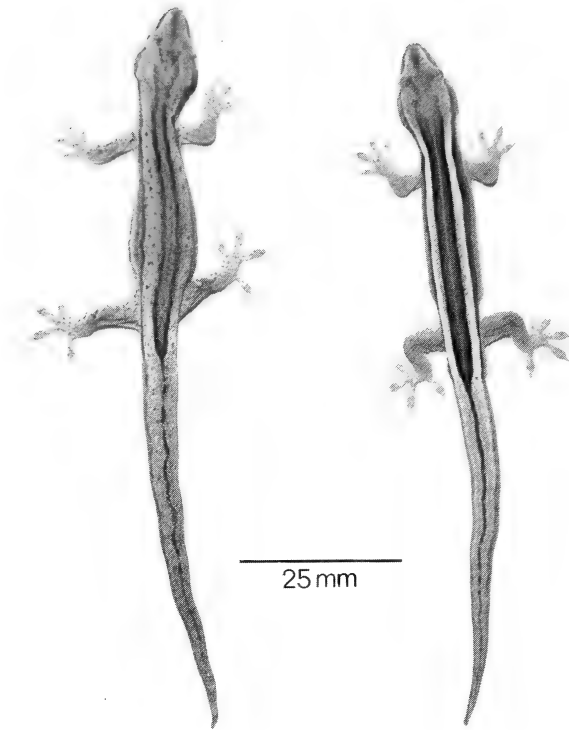bears a pattern of longitudinal stripes.

Fig.31: Two specimens of *Hoplodactylus chrysosireticus* Robb, 1980 showing variation in dorsal patterns. (Photo courtesy of B.W. Thomas)

C o m m e n t s : *Hoplodactylus chrysosireticus* was only recently recognized as a taxon distinct from *H. pacificus*. Although morphological differences between the taxa are minor, they appear to be consistent and thus warrant separation.

Newman (1980) considered the names *Hoplodactylus chrysosireticus, H. stephensi* and *Heteropholis poecilochlorus* as used by Robb (1980a) as nomina nuda. McDowall (1981), however, correctly showed that the usage of the names in Robb constitute valid descriptions. This species is distributed in coastal and central Taranaki (North Island) from Waitara to just north of Paitea and Mana Island (near Titahi Bay). It has also reportedly been discovered several hundred kilometers to the north on Motupia Island (Pickard & Towns 1988, see Fig. 34) but this record may be false (A.H. Whitaker pers. comm.). It is primarily terrestrial and nocturnal, although it frequently basks during daylight hours (Wilkinson 1981). Robb (1980a) reported that it was associated with human structures and had not been found in native bush. It has also been found in *Knipholia* and flax (Robb 1980b; Wilkinson 1981). Maximum size is 70 mm SVL (Robb 1980a). Diet consists of flies, moths, earwigs, spiders and woodlice (Robb 1980a; Wilkinson 1981). Like all *Hoplodactylus*, the species is viviparous. Mating takes place in April and young are born February—March (Wilkinson 1977; Rowlands 1981a). The species is listed in the New Zealand Red Data Book (Williams & Given 1981) as being of indeterminate status.

Hoplodactylus delcourti **Bauer & Russell, 1986 (Fig. 32)**

1986 *Hoplodactylus delcourti* Bauer & Russell. New Zealand J.Zool. 13:(141).
Type locality: "possibly the North Island, New Zealand".
Holotype: MMNH 1985-38.
1988 *Hoplodactylus delcorti* Towns. A Field Guide to the Lizards of New Zealand: 6
(lapsus pro *Hoplodactylus delcourti* Bauer & Russell, 1986).

D i a g n o s i s : Digits broadly dilated, scansorial; terminal scansors present on digit
one only; rostral contacts nostril; proximal portion of toe approximately three times
width of distal portion; penultimate phalanx strongly arcuate; 25 or more lamellae
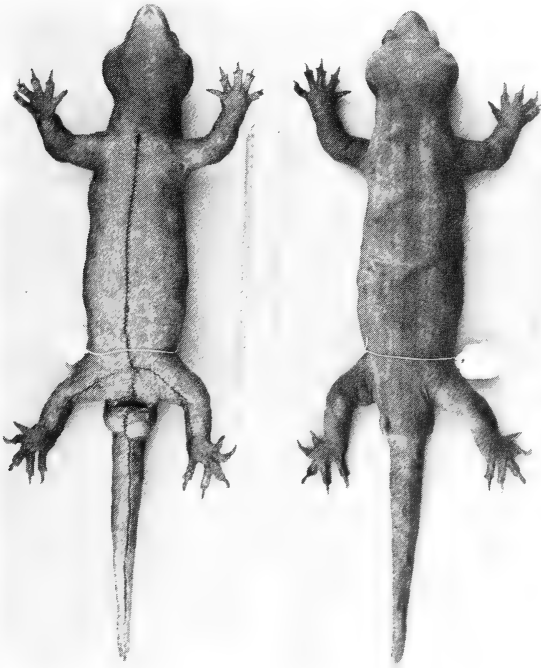under fourth toe; body striped longitudinally; huge size.

Fig.32: Ventral and dorsal views
of the Holotype of *Hoplodac-
tylus delcourti* Bauer & Russell,
1986. MMNH 1985-38 (rule = 30
cm).

C o m m e n t s : This species is known from a single, partial specimen. Its provenance
is unknown, but it has been suggested that the specimen originated from Northland
(Bauer & Russell 1986, 1987). The animal has been associated with the kawekaweau,
a reptile of Maori legend (Bauer & Russell 1987). Russell & Bauer (1986) hypothesized
that the biology of this species was probably similar to that of *H. duvaucelii* and
Whitaker (1987) suggested that it may also have been a nectivore or frugivore. The
single extant specimen has a SVL of 370 mm, making it by far the largest species of
gekkonid ever to have lived. The species is probably extinct (Bauer & Russell 1986) but
might still occur in rocky, forested regions in the northern North Island. Recent sear-
ches in the area have not located evidence for the continued existance of *H. delcourti*
(Clark 1985).

Hoplodactylus duvaucelii (**Duméril & Bibron, 1836**) (**Fig. 33**)

1836 *Platydactylus duvaucelii* Duméril & Bibron. Erpétologie Généralé vol. 3: 312.
Type locality: Bengal (Terra typica designata — Smith 1933a: "Island of Hen and Chickens, east coast of the North Island of New Zealand").
Lectotype: MNHN 5977, here designated.
Paralectotypes: MNHN 6680-1; RMNH 2722.
1843 *Hoplodactylus duvaucelii* Fitzinger. Systema Reptilium: 19,100.
1856 *Platydactylus duvaucelii* Lichtenstein. Nomenclator Reptilium et Amphibiorum Musei Zoologici Berolinensis: 4.
1859 *Naultinus pacificus* Blyth. J.Asiatic Soc. Bengal 28: 279 (nec *Naultinus pacificus* Gray, 1842)
1864 *Pentadactylus duvaucelii* Günther. The Reptiles of British India: 118.
1885 *Hoplodactylus duvaucelii* Boulenger. Catalogue of Lizards in the British Museum, vol. 1: 172.
1897 *Hoplodactylus granulatus* (part) Lucas & Frost. Trans. New Zealand Inst. 1896 29: 265.
1902 *Hoplodactylus duvancellii* Schaefer. Arch. Naturgesch. 68: 35.
1954 *Rhacodactylus trachyrhynchus* Guibé. Catalogues des Types des Lézards: 16 (ex errore pro *Hoplodactylus duvaucelii* (Duméril & Bibron, 1836); non *Rhacodactylus trachyrhynchus* Bocage, 1873).
1954 *Hoplodactylus duvaucellii* (part) Hard. Tane 6: 143.

Fig.33: Lectotype of *Platydactylus duvaucelii* Duméril & Bibron, 1836 (= *Hoplodactylus duvaucelii*). MNHN 5977. (Photo courtesy of Muséum National d'Histoire Naturelle, Paris)

1955 *Hoplodactylus duvauceli* McCann. Dominion Mus.Bull. 17: 39; pl. 3 (figs. 1—7); fig. 3. (nomen emendatum pro *Hoplodactylus duvaucelii* (Duméril & Bibron, 1836)).
1956 *Hoplodactylus duvaucelii* Stephenson & Stephenson. Trans.Roy.Soc. New Zealand 84: 341; figs. 1B,C, 2B,C, 3B, 6A,D,E.
1961 *Naultinus duvauceli* Chrapliwy et al. Herpetologica 17: 7.
1961 *Hoplodactylus duvaucelii* Myers. Herpetologica 17: 171.
1966 *Hoplodactylus duvauceli* Sharell. The Tuatara, Lizards and Frogs of New Zealand: 49; pls. 28, 29, 30, 31.
1967 *Hoplodactylus duvaucelii* Kluge. Bull.Amer.Mus.Nat.Hist. 135: 25.
1970 *Hoplodactylus duvaucelii* Forster & Forster. Small Land Animals of New Zealand: 16; 2 figs. (p. 16).
1988 *Hoplodactylus duvaucelii* Bauer. New Zealand J.Zool. 14 (1987): 593.

D i a g n o s i s : Supraocular portion of frontal deeply furrowed (in adults); juvenile color pattern with paravertebral longitudinal rows of light spots; cloacal spurs rounded, 1—5 in number; terminal scansors on digit one only; rostral contacts nostril; proximal portion of toe approximately three times width of distal portion; penultimate phalanx
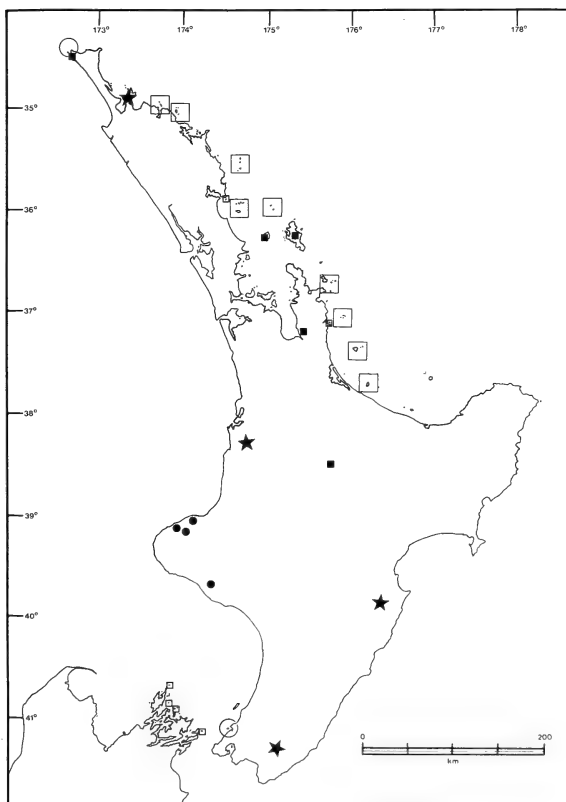

Fig.34: Distribution of *Hoplodactylus duvaucelii* (squares — modern localities, stars — subfossil sites) and *H. chrysosireticus* (closed circles) in northern New Zealand.

strongly arcuate; twenty or fewer lamellae under fourth toe; adult pattern of chevrons on dorsum. (5, 62, 95-A).

C o m m e n t s : The history of the problem of the provenance of *H. duvaucellii* was reviewed by Smith (1933a, 1933b), Stephenson (1948) and Bauer (1988). The species currently has a disjunct range including most of the northern offshore islands (summaries of distribution by island group are provided by McCallum 1982a, Bauer 1986, Towns & Robb 1986, Pickard & Towns 1988) as well as the islands of Cook Strait — Brothers (McCann 1955; Barwick 1982), Chetwode Islands (Meads 1976; McCallum 1984) and Trios Island (Werner 1901; McCann 1955; Meads 1976) (Fig 34). McCann (1955) reports a single specimen from Stephen (= Stephens) Island, but *Hoplodactylus duvaucelii* is not currently present there. It is likely that this species was once more widely distributed on the mainland of the North Island. Recent subfossil material confirms this (Worthy 1987). There is also an old, but doubtful record from Cape Maria van Diemen (McCallum 1981). The current disjunct distribution pattern is shared by *Cyclodina whitakeri* and *C. macgregori* as well as the tuatara (Towns et al. 1985).

Hoplodactylus duvaucelii has a broad range of habitats and retreats (Whitaker 1968) and has been found under ground cover and debris (Werner & Whitaker 1978; Miller 1978), in flax (Whitaker 1968; Miller 1978), *Leptospermum* (Hard 1954; Towns 1971a), under the bark of *Meterosideros excelsa* (Hard 1954), in *Macropiper excelsum* (Hard 1954), on boulder beaches and cliffs (Porter 1982), and in forest fringe vegetation (Whitaker 1968). It has also been reported from the burrows of petrels (Whitaker 1968) and tuataras (McCann 1955; Forster & Forster 1970). Subfossil evidence, however, suggests that forested habitats were occupied by *H. duvaucelii* 3000—4000 ybp (Worthy 1987). Whitaker (1973, 1978) indicates that this species is particularly vulnerable to the effects of the introduced kiore *(Rattus exulans)* and, on islands with kiore, is usually only found in crevices on cliff faces (Fig. 35). It is generally rare or absent on islands of less than one hectare in area (Whitaker 1973; McCallum 1982b).

This is the largest living New Zealand gecko with a maximum SVL of 160 mm (Whitaker 1968). Specimens from the northern islands are generally larger than those from Cook Strait (Whitaker 1968; Barwick 1982). Animals in the Poor Knights generally became active about 30 minutes after sunset, reached peak activity at about 21:00 and began retiring by 3:30 (Whitaker 1968). The diet consists of flies, moths, grubs (Hard 1954), orthopterans, beetles (Porter 1981; Barwick 1982), small crustaceans, the fruit of kawakawa trees and pohutukawa, ngaio, and flax nectar (Whitaker 1968, 1987), a variety of plant parts and young *Hoplodactylus maculatus* (Barwick 1982). *Hoplodactylus duvaucelii* is known to forage on beaches down to the splash zone (Whitaker 1968). Both males and females on the Brothers (Cook Strait) become mature at about 95—100 mm SVL, or after about seven years (Barwick 1982). Breeding takes place in September or October and young are born between February and May (Rowlands 1981a). Whitaker's (1968) detailed ecological work demonstrated that individuals range widely and that population densities may reach 75—125/acre on Aorangi. Heavy mite infestations are common (McCann 1955; Whitaker 1968; Porter 1981; Allison 1982). Population dynamics and tail break data are discussed by Barwick

Fig.35: Typical rocky coastal cliff habitat of *Hoplodactylus duvaucelii* on Lady Alice Island, Hen and Chickens Group, Hauraki Gulf, New Zealand.

(1982) for the Brothers Islands populations of *H. duvaucelii*. McCann (1955) and Robb (1980a) discussed agressive behavior and possible family groups in the species. Protest calls of this gecko are discussed by McCann (1955).

Hoplodactylus granulatus (Gray, 1845) (Fig. 36)

1843 *Naultinus pacificus* (part) Gray. Travels in New Zealand, vol. 2: 203.
1845 *Naultinus granulatus* Gray. Catalogue of the Specimens of Lizards in the Collection of the British Museum: 273.
Type locality: New Zealand.
Lectotype: BMNH 1946.8.22.71, here designated.
Paralectotypes: BMNH 1947.8.22.70, 1946.8.22.72, 1946.9.8.13.
1863 *Hoplodactylus (Naultinus) granulatus* Hochstetter. Neu-Seeland: 429.
1870 *Naultinus greyii* Knox. Trans. New Zealand Inst. 2: 20. (lapsus pro *Naultinus grayii* Bell, 1843; nec *Naultinus grayii* Bell, 1843).

1871 *Naultinus granulatus* Buller. Trans. New Zealand Inst. 3: 9.

1872 *Naultinus pacificus* (part) Hutton. Trans. New Zealand Inst. 4: 172.

1875 *Naultinus granulatus* Günther. The Zoology of the Voyage of H.M.S. Erebus and Terror, vol.2: 17.

1881 *Naultinus sylvestris* Buller. Trans. New Zealand Inst. 13: 419.

Type locality: Wooded country of the Wanganui District, North Island (New Zealand). Holotype: not located.

1885 *Naultinus versicolor* Colenso. Trans. New Zealand Inst. 17: 149.

Type locality: Forests near Norsewood, County of Waipawa and Glenross, County of Hawke's Bay (New Zealand).

Syntypes: CMC ; NMNZ (specimens not located).

1885 *Naultinus elegans* (part) Boulenger. Catalogue of Lizards in the British Museum, vol.1: 169.

1885 *Naultinus silvestris* Boulenger. Ibid., vol. 1: 169 (ex errore in synonomy of *Naultinus elegans* Gray, 1842 pro *Naultinus sylvestris* Buller, 1881).

1885 *Hoplodactylus granulatus* Boulenger. Ibid., vol.1: 171; pl. XV (fig. 1).

1895 *Naultinus sylvestris* Buller. Trans. New Zealand Inst. 27: 93.

1904 *Dactylocnemis granulatus* Hutton & Drummond. The Animals of New Zealand: 439.

1904 *Hoplodactylus granulatus* Hutton. Index Faunae Novae Zelandiae: 39.

1905 *Naultinus sylvestris* Buller. Supplement to Birds of New Zealand: xx.

1919 *Dactylocnemis granulatus* Dore. New Zealand J.Sci. and Technol. (2)3: 164.

1929 *Naultinus elegans* (part) Martin. The New Zealand Nature Book: fig. 41 (p. 160).

1929 *Hoplodactylus granulatus* Martin. Ibid.: 162.

1936 *Haplodactylus granulatus* Falla. The Weekly News, 3 June, 1936: 57. (error typographicus pro *Hoplodactylus granulatus* (Gray, 1845)).

1948 *Hoplodactylus granulatus* Stephenson. Rec. Auckland Inst. and Mus. 3: 339.

1955 *Heteropholis nebulosus* McCann. Dominion Mus.Bull. 17: 69; pl. 7 (figs. 8—11).

Type locality: Cundy (= Kundy) Island, off (western coast of) Stewart Island (New Zealand (47°07'S, 167°33'E)).

Holotype: NMNZ R93.

1961 *Naultinus granulatus* Chrapliwy et al. Herpetologica 17: 7.

1961 *Naultinus grayi* Chrapliwy et al. Ibid.: 7. (lapsus pro *Naultinus greyii* (Knox, 1870); nec *Naultinus grayii* Bell, 1843).

1961 *Naultinus brevidactylus* Chrapliwy et al. Ibid.: 7. (nec *Naultinus brevidactylus* Grey, 1845).

1961 *Naultinus maculatus* Chrapliwy et al. Ibid.: 7. (ex errore).

1961 *Hoplodactylus granulatus* Myers. Herpetologica 17: 169.

1980 *Hoplodactylus nebulosus* Robb. New Zealand Amphibians and Reptiles in Colour: 60.

D i a g n o s i s : 2—4 inscriptional ribs; apical scansors on digit one only; digits scansorial, narrow; rostral contacts nostril; penultimate phalanx not strongly arcuate; juvenile pattern as adult; white patch between eye and ear; tail without small scale rows at autotomy septa. (32-B).

Fig.36: Lectotype of *Naultinus granulatus* Gray, 1845 (= *Hoplodactylus granulatus*). BMNH 1946.8.22.71. (Photo courtesy of British Museum (Natural History))

C o m m e n t s : The taxonomic history of this species is the most confused for any in the tribe Carphodactylini. Fifteen different names or combinations have been used since the description of the species by Gray (1845). Thomas (1981), in synonymizing *Heteropholis nebulosus* with *Hoplodactylus granulatus*, presented a summary of the history of the former name and an exhaustive synonomy of the taxon. McCann (1955) explained some of the taxonomic problems of this taxon while creating additional ones himself. Despite its unique coloration, its more slender toes and tail, and generally *Naultinus*-like post-cranial morphology, many workers have doubted the distinctness of *H. granulatus* and relegated it to the synonymy of *H. pacificus*. Others (Buller 1881; Colenso 1885) were unaware that their new taxa had been described, albeit poorly, forty years earlier. It is unclear what prompted McCann (1955) to erect *Heteropholis nebulosus* for two Stewart Island specimens of *H. granulatus*.

The species is distributed throughout most of New Zealand, with the exception of the extreme north of the North Island and the south central South Island (Pickard & Towns 1988) (McCann 1956 mistakingly believed this taxon to be limited in distribution to the North Island) (Fig. 37). Northern offshore island records include Great Barrier (Newman & Towns 1985), Little Barrier and Waiheke Island (McCallum & Harker 1982). (A doubtful record exists from Middle Island in the Mercury group, Atkinson 1964). Towns & Robb (1986) considered that this restricted distribution, like that of *Naultinus elegans*, probably reflects the requirements of this species for larger islands, capable of supporting sufficient forest growth. In the south *Hoplodactylus granulatus* occurs at elevations of up to 1700 m (Bull & Whitaker 1975) and is widely distributed on the mainland and on the islands of Cook Strait — Maud Island (Meads 1976); Chetwode Islands (McCallum 1984) and Foveaux Strait — Zero Rock, Women Island, Herekopane Island, Big Island and Kundy Island (Adams & Cheyne 1968; Thomas 1981, 1982a). Lucas & Frost (1897) cited the species as occurring on Stephens Island, but this is probably incorrect.

Hoplodactylus granulatus is regarded as primarily a forest dweller and has been found in beech forest *(Nothofagus)* (Thomas 1976), bush and shrubland (Miller & Miller 1981), and manuka (Buller 1896). Although often active at night, it may be found by
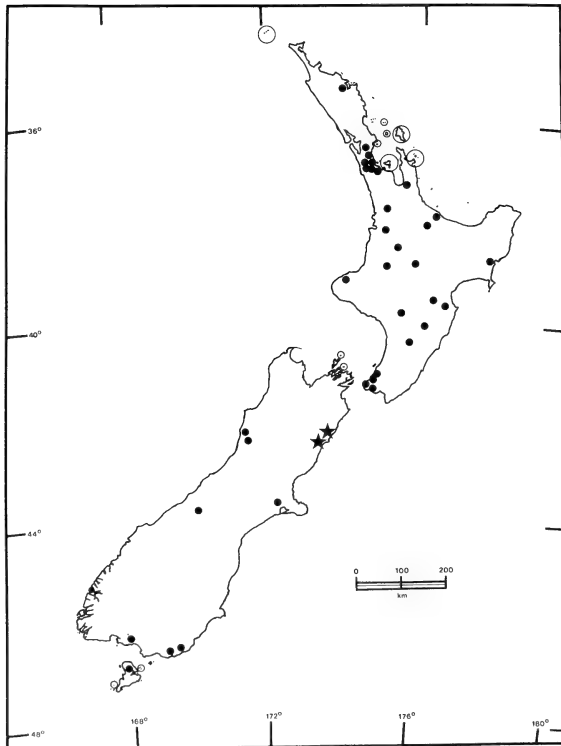

Fig.37: Distribution of *Hoplodactylus granulatus* (circles) and *H. kahutarae* (stars) in New Zealand.

day in hollows of trees (McCann 1955) or basking (Robb 1980a). Rowlands (1975a) stated that the species is crepuscular. Maximum size is 89 mm SVL (ZMH R02821). The diet consists mainly of insects. McCann (1955) and Rowlands (1981a) have discussed captive feeding habits. This species is taken by kingfishers *(Halcyon sancta)* among other predators (Fitzgerald et al. 1986). Rowlands (1981a) reported bimodal mating periods in captivity and young are generally born in mid- to late summer (Robb 1980a; Rowlands 1981a). Copulation was described by Edney (1970). Mites are common parasites on this species (Buller 1880; Colenso 1880). This species is not currently protected under the New Zealand Wildlife Act.

Hoplodactylus kahutarae **Whitaker, 1985 (Fig. 38)**

1985 *Hoplodactylus kahutarae* Whitaker. New Zealand J.Zool. 11 (1984): 260; figs. 2—4.
Type locality: 1380 m, on west side of Kahutara Saddle, Seaward Kaikoura Range (42°19'22"S, 173.°26'06"E) South Island, New Zealand.
Holotype: NMNZ R1980.

Fig.38: Living female *Hoplodactylus kahutarae* Whitaker, 1985. SVL = 85 mm.

D i a g n o s i s : Limbs and toes elongate; no terminal scansors on any digits; digits scansorial, narrow; prominent supraciliary scales; mouth lining yellowish; peritoneum black; eye black; preanal pores not extending onto thighs.

C o m m e n t s : This species, first discovered in 1970 (Whitaker 1985), is, in many respects, atypical of members of the genus. *Hoplodactylus kahutarae* is known only from Mt. Tarahaka and Kahutara Saddle in the Seaward Kaikoura Range on the east coast of the South Island (Fig. 37). The habitat is described in detail by Whitaker (1985). Specimens have been found at altitudes of 1300 m in sub-alpine habitats of solid rock bluffs (Fig. 39). Animals are active at temperatures as low as 7 °C (Whitaker 1985) and bask frequently at temperatures above 13 °C. Nothing is known of its biology in the wild, although in captivity this species feeds on a variety of small arthropods (B.W. Thomas pers. comm.). Newman (1982) listed the species as having a high conservation priority largely because of its restricted range.
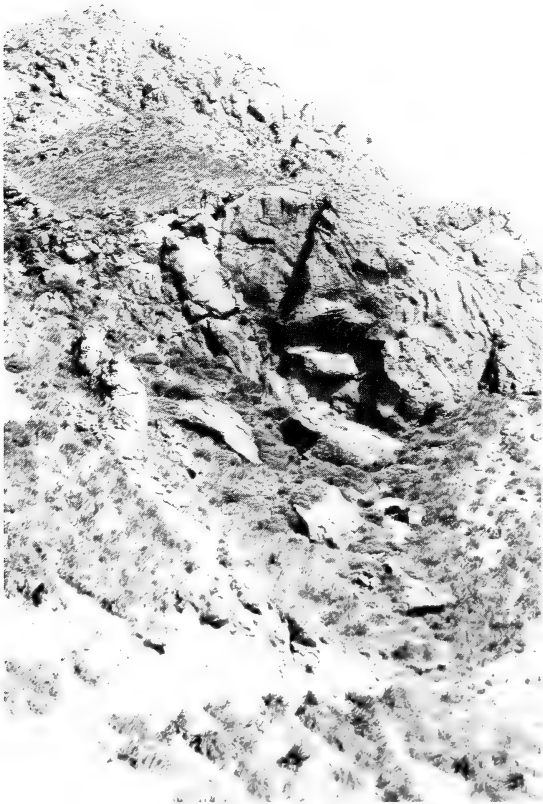

Fig.39: Subalpine habitat of *Hoplodactylus kahutarae* in the Seaward Kaikoura Range, South Island, New Zealand (elevation approx. 1300 m). (Photo courtesy of A.H. Whitaker)

Hoplodactylus maculatus **(Gray, 1845) (Figs. 40,41)**

1845 *Naultinus maculatus* Gray. Catalogue of the Specimens of Lizards in the British Museum: 273.
Type locality: New Zealand.
Lectotype: BMNH 1946.9.8.14, here designated.
Paralectotype: BMNH 1946.9.8.15.
1871 *Naultinus pacificus* (part) Buller. Trans.New Zealand Inst. 3: 7.
1871 *Naultinus granulatus* (?) Buller. Ibid.: 9. (fide Robb & Rowlands 1977).
1872 *Naultinus pacificus* (part) Hutton. Trans.New Zealand Inst. 4: 172.
1885 *Hoplodactylus maculatus* Boulenger. Catalogue of the Lizards in the British Museum, vol.1: 171; pl. XIV (fig. 1).
1901 *Woodworthia digitata* Garman. Bull.Mus.Comp.Zool. 39: 4; pl. 1 (figs. 2, 2a—f).
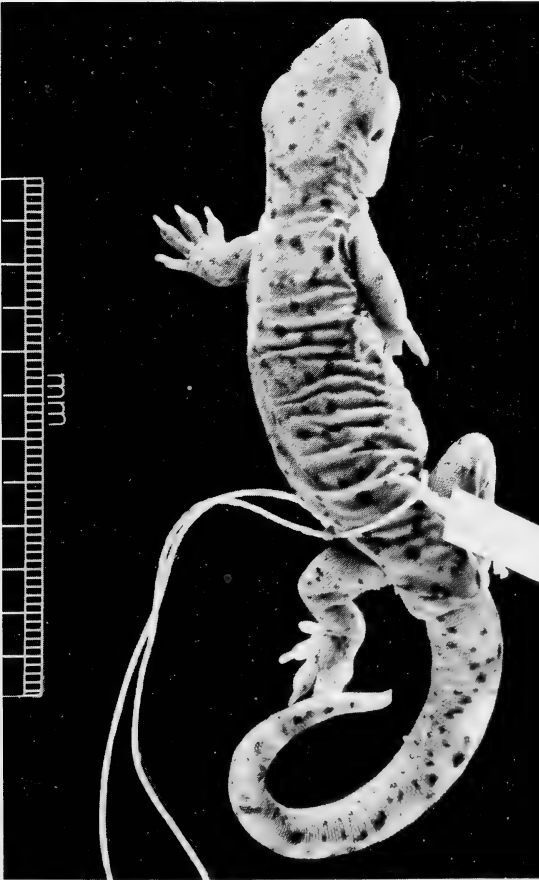Type locality: New Zealand.

Fig.40: Lectotype of *Naultinus maculatus* Gray, 1845 (= *Hoplodactylus maculatus*). BMNH 1946.9.8.14. (Photo courtesy of British Museum (Natural History))

Syntypes: MCZ 6153, 152218.

1955 *Hoplodactylus pacificus* (part) McCann. Dominion Mus.Bull. 17: 44; fig. 6.

1961 *Naultinus pacificus* (part) Chrapliwy et al. Herpetologica 17: 7.

1961 *Hoplodactylus pacificus* (part) Myers. Herpetologica 17: 169.

1965 *Hoplodactylus digitatus* Wermuth. Das Tierreich 80: 94.

1965 *Hoplodactylus pacificus* (part) Wermuth. Ibid.: 95.

1977 *Hoplodactylus maculatus* Robb & Rowlands. Rec.Auckland Inst.Mus. 14: 139; figs. 2,4,6,8,10.

D i a g n o s i s : Terminal scansors on digit one only; rostral excluded from nostril; rostral 2 times broader than deep; digits scansorial, broadly expanded; peritoneum lightly pigmented; mouth lining and tongue pinkish; juvenile pattern as adult; preanal organs extending on to thighs. **(79).**

C o m m e n t s : This species has only recently been resurrected from the synonymy of *Hoplodactylus pacificus* (Rowlands 1977; Robb & Rowlands 1977). It is now generally recognized that *H. maculatus* as now construed is actually a species complex (B.W. Thomas pers. comm.) with perhaps three or more specific level subunits. Although differentiated little in morphology, these forms have distinct size, breeding and behavioral peculiarities. Because the revision of the complex is incomplete I have treated all of these forms as a single species because all members of the complex appear, on preliminary morphological and biochemical grounds, to form a monophyletic group.

Fig.41: Large group of *Hoplodactylus maculatus* under communal cover in the Keeper's Bush, Stephens Island, Cook Strait, New Zealand.
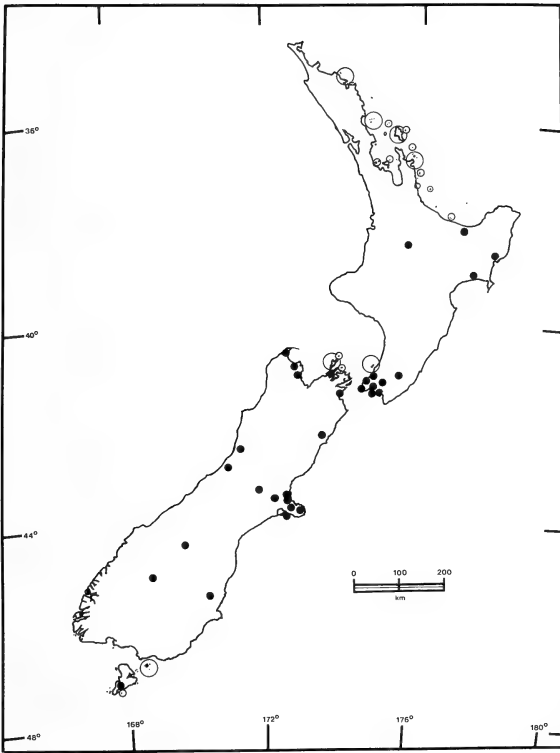
Fig.42: Distribution of *Hoplo-dactylus maculatus* in New Zea-land.

It should be noted that the confusion of this species with *H. pacificus* has caused some problems with the interpretation of biological data. In many cases in which specimens are not available to confirm species identification, the name *pacificus* may refer to *maculatus*. When only the latter occurs the interpretation is obvious, but in areas of sympatry (most of the North Island) this determination cannot be made. Such references are discussed in the comments for *H. pacificus*. In most cases statements apply to both species.

H. maculatus is distributed throughout New Zealand with the possible exception of the North Cape region (McCallum 1981, but see Pickard & Towns 1988) and a number of offshore islands (Fig. 42). Known island localities include D'Urville Island (Buck-ingham & Elliott 1979), Stephens Island (Werner 1901; Walls 1983), Trios Island (Werner 1901) and the Stephenson Island group (McCallum 1982b) in Cook Strait, Bird Island and Green Island (Foveaux Strait) (Thomas 1982a) and many northern islands (McCallum 1982a; Bauer 1986; Towns & Robb 1986). Notable island groups lacking this species are the Poor Knights, Three Kings, Mokohinaus and Stewart Island proper (there is a single, doubtful record from Stewart Island — SMI E81.3/1—3). On all nor-thern island groups except Whale Island, *H. maculatus* is sympatric with *H. pacificus*.

Everywhere it occurs, *H. maculatus* is the most plentiful gecko. It is not protected under the New Zealand Wildlife Act. The species is found from sea-level to 1700 m (Bull & Whitaker 1975). It lives a wide variety of habitats and has been found in association with exfoliating rocks (Miller & Miller 1981; McCallum 1982b), under stones (Thomas 1976; Werner & Whitaker 1978; Buckingham & Elliott 1979; Walls 1983), in tree hollows and under bark (Towns 1971b; Walls 1983) on steep rock faces and road cuttings (Buckingham & Elliot 1979; Walls 1983) and in flax (Cawthorn 1972). It is sometimes active in the splash zone on the coast (Cawthorn 1972; Robb & Rowlands 1977). It is somewhat less arboreal than *H. pacificus* (Robb & Rowlands 1977; Robb 1980a). During daylight hours this gecko usually remains concealed, heating indirectly from its cover (Werner & Whitaker 1978), although direct basking is known (Cawthorn 1972; Robb 1980a). Frequently many individuals may be found together under a piece of bark, rock or debris. I have seen as many as 200 individuals under a single tin sheet on Stephens Island (Fig. 41). Whitaker (1982) estimated mainland (Turakirae Head) populations at approximately 4000 individuals/hectare. This species reaches a maximum size of 82 mm SVL (Towns 1971b). The diet is composed largely of arthropods, with spiders and mites being the most important items (Martin 1929; Whitaker 1982). The fruits of *Coprosma* and *Muehlenbeckia* also are eaten and flax nectar may be taken as well (Whitaker 1982).

Breathing and activity pattern have been studied by McIvor (1973). Walls (1983) reported activity on nights as cold as 7°C. This may be facilitated by a temperature compensation mechanism based on variable oxygen consumption rates (Grimmond & Evetts 1981). Werner & Whitaker (1978) also reported on temperature relations. Winter and possibly summer lows in activity are seen in the species (Whitaker 1982). The biochemistry of "hibernating" *H. maculatus* has also been examined (Pollock & MacAvoy 1973). This species reaches sexual maturity in about the fourth year at Wellington (Whitaker 1982). Mating occurs in April or May and young are born February — May (Rowlands 1981a). Aspects of reproduction and the sexual cycle have been examined by Fawcett (1972) and Boyd (1940, 1942). Mating behavior has been outlined by Rieppel (1973, 1976b). Individuals may live up to 17 or more years (Anastasiadis & Whitaker 1987). Predators include rats, mice, hedgehogs, cats, gulls, kingfishers, harriers, moreporks, herons (Whitaker 1982), *H. duvaucelii* (Barwick 1982) and tuataras (Crook 1975; Walls 1981). Benson (1976) used circadian rhythms to suggest the separation of *maculatus* from *pacificus*. Hardy (1975) discussed the karyotype of *H. maculatus*.

Hoplodactylus pacificus (Gray, 1842) (Fig. 43)

1842 *Naultinus pacificus* Gray. Zool.Misc.: 58.
Type locality: South Sea Islands.
Lectotype: BMNH 1946.8.22.67, here designated.
Paralectotype: BMNH 1946.8.22.65.
1842 *Naultinus pacifica* Gray. Ibid.: 72.
1843 *Naultinus pacificus* (part) Gray. Travels in New Zealand: 203.

1843 *Platydactylus duvaucelii* Gray. Ibid.: 203. (nec *Platydactylus duvaucelii* Duméril & Bibron, 1836).

1845 *Naultinus pacificus* (part) Gray. Catalogue of the Specimens of Lizards in the British Museum: 169.

1851 *Platydactylus pacificus* Duméril. Catalogue Méthodique de la Collection des Reptiles: 35 (nec *Platydactylus pacificus* Duméril, 1851 ad Bavay 1869).

1857 *Hoplodactylus pomarii* Girard. Proc.Acad.Nat.Sci. Philadelphia 8: 197.

Type locality: New Zealand.

Holotype: USNM 5690.

1858 *Gehyra oceanica* (part) Girard. Herpetology of the United States Exploring Expedition: 273.

1861 *Dactylocnemis wüllerstorfii* Fitzinger. Österr.Akad.Wissensch. Math.-nat. Klasse 42: 400. (nomen nudum).

1867 *Dactylocnemis pacificus* Steindachner. Reptilien. Reise der Fregatte Novara: 11.

1868 *Pentadactylus brunneus* Cope. Proc.Acad.Nat.Sci. Philadelphia 20: 320 (synonymy fide Kluge 1965b).
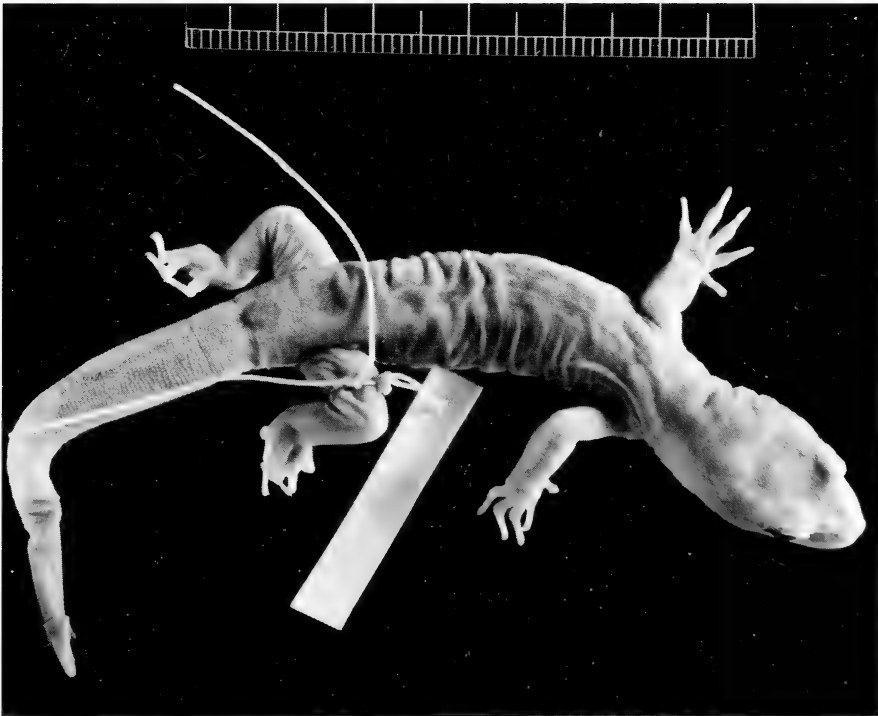

Fig.43: Lectotype of *Naultinus pacificus* Gray, 1842 (= *Hoplodactylus pacificus*). BMNH 1946.8.22.67. (Photo courtesy of British Museum (Natural History))

1871 *Naultinus pacificus* (part) Buller. Trans. New Zealand Inst. 3: 7.

1872 *Naultinus pacificus* Hutton. Trans. New Zealand Inst. 4: 172.

1885 *Aelurosaurus brunneus* Boulenger. Catalogue of Lizards in the British Museum, vol. 1: 74.

1885 *Hoplodactylus pacificus* Boulenger. Ibid.: 173.

1885 *Aeluroscalobotes brunneus* Boulenger. Ann.Mag.Nat.Hist. (5)16: 387.

1924 *Hoplodaetylus pacificus* Lord & Scott. Animals of Tasmania: 109 (lapsus pro *Hoplodactylus pacificus* (Gray, 1842)).

1954 *Hoplodactylus duvaucellii* (part) Hard. Tane 6: 143.

1955 *Hoplodactylus pacificus* (part) McCann. Dominion Mus.Bull. 17: 44; figs. 4—5.

1961 *Naultinus pacificus* (part) Chrapliwy et al. Herpetologica 17: 7.

1961 *Hoplodactylus pacificus* (part) Myers. Herpetologica 17: 169.

1977 *Hoplodactylus pacificus* (part) Robb & Rowlands. Rec. Auckland Inst.Mus. 14: 137; figs. 1,3,5,7,9.

1980 *Hoplodactylus pacificus* Robb. Rec.Natl.Mus. New Zealand 1: 308.
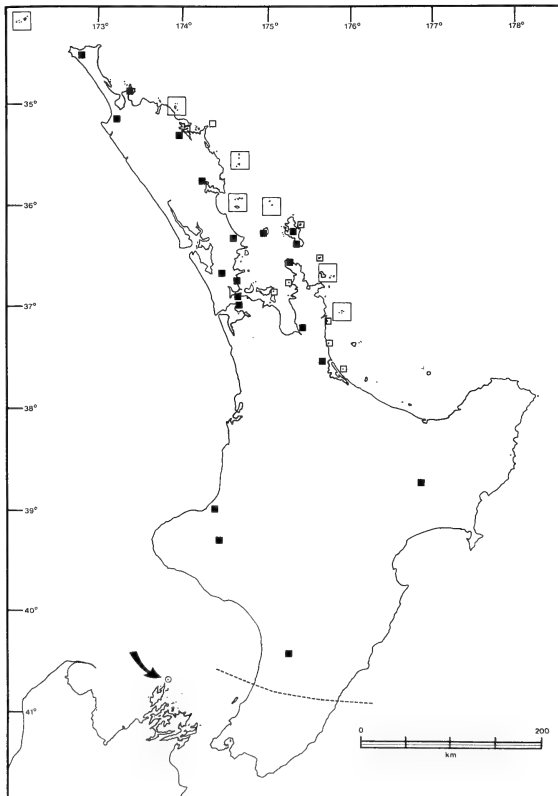
Fig.44: Distribution of *Hoplodactylus pacificus* (squares) and *H. stephensi* (circle indicated by arrow) in the North Island of New Zealand. Dashed line represents the southern extent of the range of *H. pacificus* according to Robb (1980a).

D i a g n o s i s : Digits scansorial, broadly dilated, proximal portion approximately twice width of distal; penultimate phalanx arises from within pad; approximately 12 scale rows on free portion of digit IV of pes; mouth lining and tongue pinkish; juvenile pattern as adult; preanal pores do not extend on to thighs. (93).

C o m m e n t s : The systematic confusion surrounding this species and *H. maculatus* has already been discussed. The naming of *H. pomarii* Girard, 1857 seems to have resulted from the uncertainty of the identity of *H. pacificus* as the original description was very sketchy. Fitzinger's (1861) *Dactylocnemis wüllerstorfii* is a nomen nudum; his reference to this animal as a house gecko is certainly incorrect. The systematic status and redescription are provided by Robb & Rowlands (1977). At various times *H. maculatus, H. chrysosireticus* and *H. stephensi* were all subsumed under this name as well.

The species is distributed over most of the North Island as far south as Palmerston North — 40°40'S (but see Pickard & Towns 1988 for a Wellington locality) and occurs on most of the northern offshore islands (Towns & Robb 1986; Bauer 1986) (Fig. 44). It is not known from any South Island localities or any of the islands of Cook Strait. The Stephens Island specimens mentioned by Sharell (1966) and Robb & Rowlands (1977) have since been referred to *H. stephensi*.

Like *H. maculatus*, this species occurs in a wide range of habitat types including beach rocks, wrack or driftwood (McCann 1955; Miller 1978; pers. obs.), in cliff crevices (McCallum 1980) or in forested or scrub situations, either on trees, under bark or under ground debris (Whitaker 1968; Robb & Rowlands 1977; McCallum & Harker 1982). Whitaker (1968) also found this species in petrel burrows and occasionally found this species sharing a retreat with *H. duvaucelii*. The "oceanic" gecko from North Cape that was reported to run from beach wrack into the ocean to avoid capture (Browne 1946) is probably this species. Whitaker (1968, 1973) found this species rare or absent on islands with kiore. If present, populations were small and were found only in association with steep rocky cliffs. This species is generally larger (maximum SVL 94 mm — Whitaker 1968), but more gracile than *H. maculatus*. On Aorangi, *H. pacificus* occasionally basks during daylight hours and forages at dusk, at which time they frequently climbed pohutukawa trees (Whitaker 1968). Animals remain active until about 4:30. Dietary items include a variety of insects and arthropods (Rowlands 1975b), crustaceans (McCann 1955; Whitaker 1968), kawakawa fruit and pohutukawa, ngaio and flax nectar (Whitaker 1968, 1987). Whitaker (1968) reported 50 individuals in a single pohutukawa feeding on nectar. In turn, this species is preyed upon by tuataras, kingfishers, harriers and cats (McCann 1955; Whitaker 1968; Gibb et al. 1969). The preadators listed for *H. maculatus* probably all are potential predators of this species as well. This species mates March — May and gives birth to two young in February — March (McCann 1955; Robb 1980a; Rowlands 1981a). Whitaker (1968), in his superb ecological study, relates an escape behavior in which an individual dove into a pool of water and remained submerged for more than 14 minutes while holding on to a rock; other aspects of ecology and behavior are covered in this paper as well.

Hoplodactylus rakiurae **Thomas, 1981 (Fig. 45)**

1981 *Hoplodactylus rakiurae* Thomas. New Zealand J.Zool. 8: 33; figs. 2—4.
Type locality: Southern Tin Range, Stewart Island (47°08'30"S 167°44'30"E), New Zealand.
Holotype: NMNZ R1825.

D i a g n o s i s : Abdominal ribs 5—6; terminal scansors present on all digits; digits scansorial, narrow; dorsal scales conical; tail short; juvenile and adult pattern of complex harlequin design; mouth, tongue and peritoneum darkly pigmented. (33-A).

Fig.45: Living specimen of *Hoplodactylus rakiurae* from Stewart Island, New Zealand. Note the unique coloration pattern. SVL = 60 mm. (Photo courtesy of B.W. Thomas)

C o m m e n t s : This striking species was first collected in 1969 (Thomas 1981). Thomas' (1981) description is excellent and is a good general statement of all that is known about the biology of this species. *Hoplodactylus rakiurae* is known only from the southern part of Stewart Island (Fig. 46). The species has been found under rocks and basking on moss but in captivity is active at night in foliage (Thomas 1981). In general, vegetation near known localities is composed of a variety of windshorn scrub plants, including manuka and other divaricating shrubs (Thomas 1981). At SVL 64 mm (Thomas 1981) this is the smallest species of New Zealand carphodactyline. Thomas (1981) lists a variety of insects and amphipods as well as nectar as potential food for *H. rakiurae*. Introduced rats and cats have been cited as possible predators (Thomas 1982a). The species is classified as rare (Williams & Given 1981).
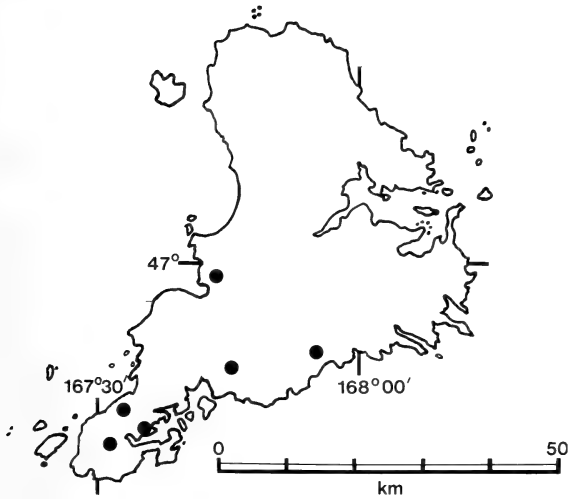
Fig.46: Distribution of *Hoplo-dactylus rakiurae* on Stewart Island, New Zealand.

Hoplodactylus stephensi Robb, 1980

1977 *Holplodactylus pacificus* (part) Robb & Rowlands. Rec. Auckland Inst. Mus. 14: 137.

1980 *Hoplodactylus stephensi* Robb. New Zealand Amphibians and Reptiles in Colour: 60; pl.12 (lower left and right).

1980 *Hoplodactylus stephensi* Robb. Rec.Natl.Mus. New Zealand 1: 308, fig. 1B.

Type locality: Stephens Island, New Zealand.

Holotype: NMNZ R1858.

D i a g n o s i s : Digits scansorial, broadened, proximal portion approximately twice width of distal portion; penultimate phalanx arises from within pad; 7 rows on free portion of digit IV of pes; 6—9 rows of preanal pores in males; peritoneum brown; tongue pink; mouth lining distinctly pigmented. (**63**, 64, 66-A).

C o m m e n t s : This species was previously considered to be part of *H. pacificus*. *Hoplodactylus stephensi* occurs only on Stephens Island in Cook Strait (Fig. 44) and thus has perhaps the most limited distribution of any gekkonid species in the world, and is considered rare and vulnerable (Williams & Given 1981). Towns et al. (1985) consider the existing population to represent a relict population. It would, however, seem more plausible that the species represents a recent offshoot from *pacificus-maculatus* stock.

Robb (1980a) stated that this species was strongly nocturnal and that its daytime retreats were in hollows or under bark in or near forested areas of the island. I have observed the species, however, active on an overcast day in divaricating shrubs on an exposed hillside on Stephens Island. Maximum SVL is 80 mm (Robb 1980b). Nothing is known of the natural diet of this species but it is probably similar to *H. maculatus* in similar regions of New Zealand. Mating takes place in spring and two live young are

born in late summer or early autumn (Robb 1980b). Sharell (1966) stated that the "Stephens Island *H. pacificus*" was a prey item in the diet of *Sphenodon punctatus*, although it is unclear whether this is in reference to *H. stephensi* or sympatric *H. maculatus*.

Naultinus Gray, 1842

1842 *Naultinus* (part) Gray. Zool. Misc.: 72.
Type species: *Naultinus elegans* Gray, 1842 (fide Myers 1961).
1882 *Heteropholis* Fischer. Abh.Naturwiss.Ver. Bremen 7: 236. (nomen novum pro *Naultinus* (part) Gray, 1842).
Type species: *Heteropholis rudis* Fischer, 1882 by monotypy.
1961 *Naultinulus* Chrapliwy et al. Herpetologica 17: 7. (nomen novum pro *Naultinus* Gray, 1842 (part)).
1961 *Naultinus* Myers. Herpetologica 17: 169.

S p e c i e s   r e f e r r e d : *Naultinus elegans* Gray, 1842; *N. gemmeus* (McCann, 1955); *N. grayii* Bell, 1843; *N. manukanus* (McCann, 1955); *N. poecilochloris* (Robb, 1980); *N. rudis* (Fischer, 1882); *N. stellatus* Hutton, 1872; *N. tuberculatus* (McCann, 1955).

D i a g n o s i s : (Node 10) A monophyletic taxon diagnosed by the following characters: pectoral girdle largely cartilaginous; green pigmentation present; metatarsals II and IV parallel; metatarsal length (shortest to longest) V-I-IV-II-III; lateral pair of cloacal bones present; mouth lining and tongue distinctly pigmented; peritoneum jet black; pupil vertical with smooth margins; diurnal; external ear generally minute; digits narrow with scansorial pads; terminal scansor single, cleft; webbing between toes absent; preanal pores present, extend on to thighs; autotomy limited to anterior post-pygal vertebrae; tail elongate and prehensile, without scansors; live bearing. (29-A, 35*, 60*, 67*).

C o m m e n t s : Great controversy has surrounded this genus since its erection by Gray (1842a, 1842b). Initially the genus included both the New Zealand green and brown geckos. Subsequent usage has restricted the name *Naultinus* to the green geckos. Chrapliwy et al. (1961), Myers (1961), Robb & Hitchmough (1980) and Whitaker (1982) have reviewed the history of the taxonomy of this genus in detail. Primary confusion has resulted from the fact that the first species in the genus *Naultinus* was in fact the brown gecko *Hoplodactylus pacificus*. Chrapliwy et al. (1961) attempted to substitute the new name *Naultinulus* for the green geckos and reinstate *Naultinus* for the members currently in *Hoplodactylus*. This was rejected both on the grounds of nomenclatural stability and adherence to the International Code of Zoological Nomenclature (Myers 1961). Thomas (1982b) listed reliable characters for separating *Naultinus* (sensu lato) and *Hoplodactylus*.

A second point of contention has been the use of the name *Heteropholis* for the South Island green geckos. First proposed by Fischer (1882), this name was largely in disuse until resurrected by McCann (1955). Traditionally, all South Island day geckos were

referred to *N. elegans*. Since 1955, the use of *Heteropholis* for South Island species has been more or less universal. Robb (1982) suggested that this usage be maintained, while Thomas (1982b), citing a lack of diagnostic characters to separate the genera, synonymized *Heteropholis* with *Naultinus*. Meads (1982), taking a more extreme view, indicated the captive production of fertile offspring from a variety of mixed crossings and advocated synonymizing all New Zealand green geckos with *N. elegans*. The latter view appears to be unwarranted because the taxa involved, although potentially inter-breeding, are spatially, and in some cases, temporally separated. Thomas' (1982b) generic synonymy, however, is consistent with the results of this study and should be adopted. Robb & Hitchmough (1980) provided a systematic review of the North Island species including partial synonomies and new diagnoses and descriptions. Hitchmough (1982a) also presented a summary of morphological and distributional data for the members of the genus. McCann's (1955) "The Lizards of New Zealand" is the most recent systematic treatment of the South Island species.

The genus as a whole ranges from the North Cape region to Southland and perhaps to Stewart Island. No species occur on the northern offshore islands (except Great and Little Barrier Islands) or on large portions of the South Island, notably Fiordland and the Southern Alps (Pickard & Towns 1988). In general, all species are diurnal and are associated with a variety of bushes and small trees. McCann (1955), Sharell (1966) and Robb (1980a) reviewed the biology of the constituent species. Captive care, including information on feeding, reproduction and parasites, has also been discussed (Rowlands 1981b; Hume 1974, 1976; Hardy 1972; Allison 1982). All *Naultinus* are ovoviviparous and typically give birth to two young. All species in the genus are protected by the New Zealand Wildlife Act of 1983.

Key to the Species of *Naultinus*

1a. Scalation of dorsal body surface homogeneous 2
b. Scalation of dorsal body surface heterogeneous 3
2a. Dome shaped scales on snout, 3 or more post-mental scales .... *N. elegans*
b. Scales of snout flat, usually 2 post-mentals .... *N. grayii*
3a. Scales heterogeneous on body and head 4
b. Head and nape only with heterogeneous conical scales 5
4a. Entire body covered by enlarged, conical scales .... *N. rudis*
b. Enlarged scales only on head and along mid-dorsal line (nape and sacrum only in Stephens Island specimens) .... *N. manukanus*
5a. Scales of body generally granular 6
b. Scales of body generally conical or tuberculate 7
6a. Supraciliary scales conical (Fig. 47) .... *N. gemmeus*
b. Supraciliary scales granular .... *N. stellatus*
7a. Scales of body flat .... *N. tuberculatus*
b. Scales of body pointed .... *N. poecilochloris*
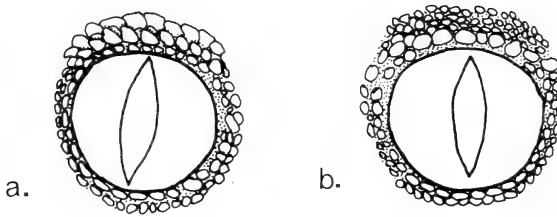
Fig.47: Circumorbital scalation of (a) *Naultinus gemmeus* and (b) *Naultinus stellatus* showing conical and granular supraciliaries, respectively (couplet 6 of *Naultinus* key).

Naultinus elegans Gray, 1842 (Fig. 48)

1842 *Naultinus elegans* Gray. Zool. Misc.: 72.
Type locality: Auckland, New Zealand.
Holotype: BMNH 1946.8.22.36.
1843 *Naultinus punctatus* Gray. Travels in New Zealand, 2. The Fauna of New Zealand: 204.
Type locality: New Zealand.
Holotype: BMNH 1946.8.22.38.
1851 *Gymnodactylus elegans* Duméril. Catalogue Méthodique de la Collection des Reptiles: 43.
1861 *Hoplodactylus elegans* Fitzinger. Österr.Akad.Wissensch. Math.-nat. Klasse 42: 400.
1861 *Hoplodactylus punctatus* Fitzinger. Ibid.: 400.
1867 *Naultinus elegans* (part) Steindachner. Reptilien. Reise der Fregatte Novara: 19.
1867 *Naultinus punctatus* Steindachner. Ibid.: 20.
1871 *Naultinus sulphureus* Buller. Trans.Proc. New Zealand Inst. 3: 8.
Type locality: Rotorua, North Island, New Zealand. (Hutton 1872 stated that the true type locality was Maketu, Buller 1872 maintained that the "Hot Springs" (= Rotorua) was correct).
Holotype: NMNZ (specimen number unknown).
1880 *Naultinus pentagonalis* Colenso. Trans.Proc. New Zealand Inst. 12: 262.
Type locality: Hampden, North Island, New Zealand.
Syntypes: repository unknown.
1885 *Naultinus elegans* Boulenger. Catalogue of Lizards in the British Museum, vol. 1: 168; pl. XIV (fig. 3).
1955 *Naultinus elegans* form *elegans* (part) McCann. Dominion Mus.Bull. 17: 31, pl. II (figs. 8—14).
1955 *Naultinus elegans* form *punctatus* McCann. Ibid.: 31.
1955 *Naultinus elegans* form *sulphureus* McCann. Ibid.: 31.
1955 *Naultinus elegans* form *occelatus* McCann. Ibid.: 31.
1961 *Naultinulus elegans* (part) Chrapliwy et al. Herpetologica 17: 7.
1961 *Naultinus elegans* (part) Myers. Herpetologica 17: 169.
1966 *Naultinus sulphureus* Sharell. The Tuatara, Lizards and Frogs of New Zealand: 48; pls. 26, 27.

1980 *Naultinus elegans elegans* Robb. New Zealand Amphibians and Reptiles in Colour: 61; pls. 11 (bottom left), 13 (top and middle).

1980 *Naultinus elegans pentagonalis* Robb. Ibid.: 62; pl. 13 (bottom).

1980 *Naultinus elegans punctatus* Robb & Hitchmough. Rec. Auckland Mus. 16: 193.

D i a g n o s i s : Generally three or four abdominal ribs; dorsal scalation homogeneous; scales on snout dome shaped; three or more postmental scales. (33-B, 78).

C o m m e n t s : Gray's descriptions (1842b, 1843) are too vague to be usefull. Girard (1857) presented a good redescription of *N. punctatus*. The great variety of color patterns exhibited by members of this species resulted in numerous new taxa as seen in the synonymy above. Buller's (1871) *sulphureus*, in particular, has had a continued reappearance as amateur naturalists have continued to accord specific rank to this color phase. Robb & Hitchmough (1980) recognized two subspecies, *N. e. elegans* and *N. e. punctatus*, the former distributed from Dargaville and Whangarei south to the northern Bay of Plenty and northern Taranaki and the latter in the remaining southern parts of the North Island (Pickard & Towns 1988). Morphological differences are minor and in-
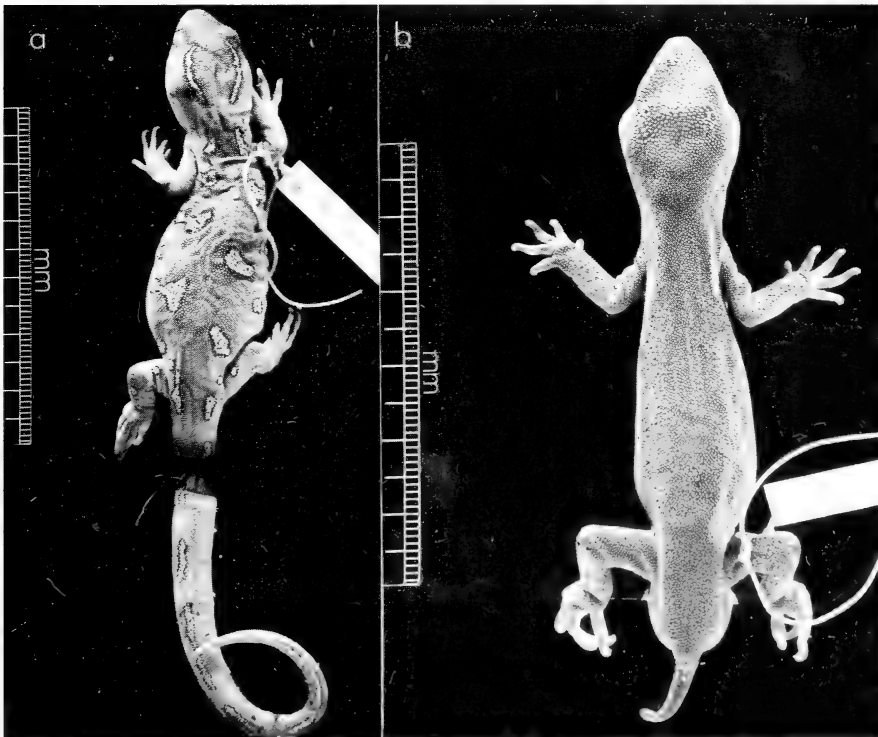

Fig.48: a. Holotype of *Naultinus elegans* Gray, 1842. BMNH 1946.8.22.36. b. Holotype of *Naultinus punctatus* Gray, 1843 (= *Naultinus elegans*). BMNH 1946.8.22.38. (Photos courtesy of British Museum (Natural History))

consistent, although differences in reproductive timing (Rowlands 1981a) suggest that the populations may warrant taxonomic distinction.

In addition to the North Island, populations (nominate subspecies) exist on Great and Little Barrier Islands in the Hauraki Gulf (Robb & Hitchmough 1980; Dick 1981; Ogle 1981) (Fig. 49). McCallum & Harker (1982) also reported *N. elegans* from inner islands of the Gulf. Gray (1843) described the habitat of *Naultinus elegans* as "amongst decayed trees and running about between the fern". Hutton (1872) recorded open fernland as the habitat. This species and its congeners are often found in manuka *(Leptospermum scoparium)* and kanuka *(L. ericoides)* (Sharell 1966; Taylor 1976; Robb 1980a). This species overwinters among roots of *Phormium* (flax) (McCann 1955) and shelters under bark or stones (Robb 1980a). The maximum size recorded for this taxon is SVL 95 mm (Robb & Hitchmough 1980). Northern individuals mate in September—November and give birth to two live young between April and September. The southern form mates and gives birth several months earlier (Rowlands 1981). Colenso (1880, 1887) was apparently the first to confirm live birth in this species and stated that gestation was five and a half months, although in reality it lasts approximately nine to eleven months (Rowlands 1979; Robb 1980a). Diet consists primarily of insects (McCann
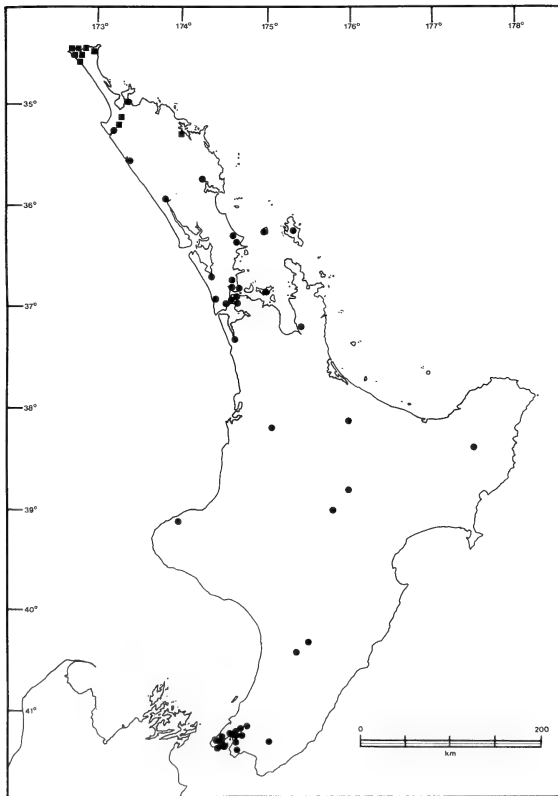

Fig.49: Distribution of members of genus *Naultinus* in the North Island of New Zealand. *Naultinus elegans* (circles), *N. grayii* (squares).

1955; Bull & Whitaker 1975) but nectar may also form part of the wild diet, McCann (1955). The call and threat display of *N. elegans* is described by McCann (1955). The Maori name for this animal is "kakariki" and like most lizards, this species was feared by the early Maori (Best 1923; Downes 1937).

Naultinus gemmeus (McCann, 1955)

1869 *Naultinus lineatus* Gray. Ann.Mag.Nat.Hist. (4)3: 243.
Type locality: Otraroa (= Akaroa) in Canterbury (South Island) New Zealand.
Holotype: BMNH (specimen number unknown).
1955 *Heteropholis gemmeus* McCann. Dominion Mus.Bull. 17: 63; figs. 9,10.
Type locality: Rangiora, South Island, New Zealand.
Holotype: CMC (specimen number unknown).
1982 *Naultinus elegans gemmeus* Meads. New Zealand Herpetology: 324.
1982 *Naultinus gemmeus* Thomas. New Zealand Herpetology: 336.
1986 *Naultinus elegans gemmeus* Gill. Collins Handguide to the Frogs and Reptiles of New Zealand: 48.

D i a g n o s i s : Dorsal scalation heterogeneous, granular; supraciliary scales conical.

C o m m e n t s : This is the most widespread of the South Island *Naultinus*. Three distinct populations exist, one on the Banks Peninsula and the Canterbury Plains, a second on the Otago Peninsula and coastal southeast and a third, isolated form from Mt. Cook (Fig. 51). Geckos from extreme southern New Zealand (Invercargill, Bluff, Green Island and Stewart Island) have been reported (Thomas 1982a) and may be referable to this species.

In general, these geckos are found in forest or scrub areas, typically on the outer foliage of divaricating shrubs two to four meters above the ground (Thomas 1982a). In Otago this species has been found in *Coprosma areolata* (Miller & Miller 1981). Henle (1981) reported on both native plants and on introduced *Pinus radiata*. Although generally assumed to be diurnal (Robb 1980a), McCann (1955) reports that captives were generally inactive during the day except for periods of basking. Maximum size is SVL 80 mm (Robb 1980a). The species mates in September—October and gives birth between February and May (Robb 1980a; Rowlands 1981a). Specimens from the Banks Peninsula are sexually dichromatic, with females being green and males brown or gray in background coloration (Thomas 1982a). There is no dichromatism among the Otago specimens. Offspring of a *N. gemmeus x N. rudis* cross showed dichromatism (Meads 1982). Wild diet is similar to that reported for the previous species (Robb 1980a).

Naultinus grayii Bell, 1843 (Fig. 50)

1843 *Naultinus grayii* Bell. The Zoology of the Voyages of H.M.S. Beagle. 27; pl.16 (fig. 2).
Type locality: Bay of Islands, North Island, New Zealand.
Holotype: BMNH 1946.9.8.16.
1858 *Naultinus graii* Girard. Herpetology of the United States Exploring Expedition: 309. (lapsus pro *Naultinus grayii* Bell, 1843).

1861 *Hoplodactylus grayi* Fitzinger. Österr.Akad.Wissensch. Math.-nat. Klasse 42: 400. (lapsus pro *Naultinus grayii* Bell, 1843).

1871 *Naultinus grayii* Buller. Trans.Proc. New Zealand Inst. 3: 7.

1885 *Naultinus elegans* (part) Boulenger. Catalogue of Lizards in the British Museum, vol. 1: 168.

1899 *Naultinus grayi* Dendy. Trans. New Zealand Inst. 31: 730.

1955 *Naultinus elegans* form *elegans* (part) McCann. Dominion Mus.Bull. 17: 31.

1961 *Naultinulus elegans* (part) Chrapliwy et al. Herpetologica 17: 7.

1961 *Naultinus elegans* (part) Myers. Herpetologica 17: 169.

1980 *Naultinus simpsoni* Robb. New Zealand Amphibians and Reptiles in Colour: 62; pls. 14, 15 (top) (nomen nudum pro *Naultinus grayii* Bell, 1843).

1980 *Naultinus grayi* Robb & Hitchmough. Rec. Auckland Mus. 16: 195; figs. 3,4,6.

1982 *Naultinus elegans grayi* Meads. New Zealand Herpetology: 324.

1982 *Naultinus grayi* Thomas. New Zealand Herpetology: 336.

1986 *Naultinus elegans grayi* Gill. Collins Handguide to the Frogs and Reptiles of New Zealand: 46.

1988 *Naultinus grayii* Bauer. New Zealand J.Zool. 14 (1987): 593.

D i a g n o s i s : Dorsal scalation homogeneous; scales on snout flat; usually two post-mental scales. (78).

C o m m e n t s : This species is similar in most respects to *N. elegans*, with which it has been frequently confused. Robb & Hitchmough (1980) resurrected this name for the green geckos of Northland, north of Whangaroa (Fig. 49). *Naultinus grayii* is unknown from offshore islands (Towns & Robb 1986). Bell (1843), whose description is adequate,

Fig.50: Holotype of *Naultinus grayii* Bell, 1843. BMNH 1946.9.8.16. (Photo courtesy of British Museum (Natural History))
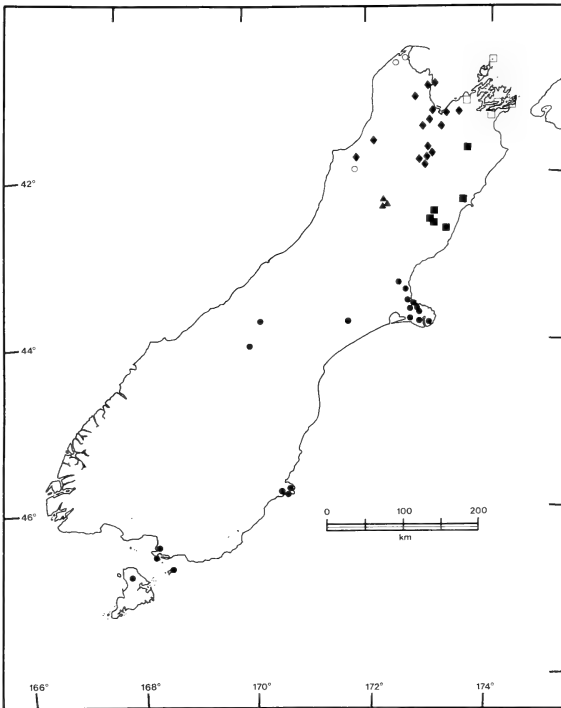
Fig.51: Distribution of members of the genus *Naultinus* in the South Island of New Zealand. *Naultinus gemmeus* (closed circles), *N. manukanus* (open squares), *N. poecilochloris* (closed triangles), *N. rudis* (closed squares), *N. stellatus* (closed diamonds), *N. tuberculatus* (open circle).

stated that this gecko lives in trees. Like most other *Naultinus*, this species typically inhabits *Leptospermum* (Robb 1980a; McCallum 1981; Hitchmough 1982b). Population density on the Karikari Peninsula was estimated at 55 individuals/hectare (Hitchmough 1982b). Maximum SVL is 95 mm (Robb & Hitchmough 1980). Food consists of a variety of insects and other arthropods (Sharell 1966). Births occur from March to June following August—September matings (Dendy 1899; Rowlands 1981a; Hitchmough 1982b). Maturity is reached after 16—17 months and females give birth at about two years (Robb & Hitchmough 1980). Ontogenetic color changes have been noted in *N. grayii* (Hitchmough 1982b). Robb (1980a) reported parental defense of young.

Naultinus manukanus (McCann, 1955) (Fig. 52)

1955 *Heteropholis manukanus* McCann. Dominion Mus.Bull. 17: 59; pl. 4 (figs. 7—11). Type locality: Marlborough Sounds, South Island, New Zealand.
Holotype: NMNZ R238.
1955 *Naultinus elegans* (part) McCann. Dominion Mus.Bull. 17: 29.
1982 *Naultinus elegans manukanus* Meads. New Zealand Herpetology: 324.
1982 *Naultinus rudis* (part) Thomas. New Zealand Herpetology: 336.
1986 *Naultinus elegans manukanus* Gill. Collins Handguide to the Frogs and Lizards of New Zealand: 48.

Fig.52: *Naultinus manukanus* (McCann, 1955) exhibiting tail prehension, Stephens Island, Cook Strait, New Zealand. SVL = 62 mm.

D i a g n o s i s : Dorsal scalation heterogeneous, at least on head, nape and sacral region, but never on entire body; rostral contacts nostril. (79).

C o m m e n t s : Thomas (1982b) considered this species to be conspecific with *N. rudis* and indicated that the morphocline first reported by Bull & Whitaker (1975) was indeed present. I have examined only specimens from Stephens Island which are quite distinct from *N. rudis* and therefore favor the specific distinction of the two taxa.

Naultinus manukanus is distributed throughout the Marlborough Sounds and on Stephens Island and D'Urville Island (Buckingham & Elliott 1979) (Fig. 51). The species is found chiefly in manuka and kanuka (Robb 1980a) but I have observed them on a variety of small divaricating shrubs on Stephens Island (Fig. 53). They are also known from heights of 0.5 to 1.5 m in taupata *(Coprosma repens)* (Werner & Whitaker 1978). Walls (1983) reported that the species was fairly common on Stephens Island and that specimens there showed summer peaks and winter troughs of activity. The maximum SVL is 68 mm (Robb 1980a). The diet consists of insects and other small invertebrates (Robb 1980a). *Naultinus manukanus* mates from June to October and gives birth in March or April (Rowlands 1981a). Habitat destruction in the Marlborough Sounds appears to be having a negative effect on the populations there (Robb 1980a).

Fig.53: Stands of native vegetation, Stephens Island, Cook Strait, New Zealand. Habitat of *Hoplodactylus stephensi, Naultinus manukanus* and *Sphenodon punctatus*.

Naultinus poecilochlorus (Robb, 1980)

1980 *Heteropholis poecilochloris* Robb. New Zealand Amphibians and Reptiles in Colour: 67; pl. 19.
1980 *Heteropholis poecilochlorus* Robb. Rec.Natl.Mus. New Zealand 1: 309; fig. 1C.
Type locality: Lewis Pass, South Island, New Zealand.
Holotype: NMNZ R1862.
1982 *Naultinus elegans poecilochlorus* Meads. New Zealand Herpetology: 324.

D i a g n o s i s : Dorsal scalation of head and nape heterogeneous; scales conical, pointed.

C o m m e n t s : This species is restricted to a small area in south Nelson — north Canterbury centered around Lewis Pass from Rahu to Reefton (Robb 1980b) (Fig. 51). It is separated from the range of *N. stellatus* by a mountainous region. It is associated with shrubs in and around *Nothofagus* forests (Robb 1980b; Henle 1981). *Naultinus poecilochloris* has been found in *Leptospermum scoparium, Discaria toumatou, Rubus* spp. and *Gahnia* sp. (Robb 1980b). The species occurs above the winter snow line and apparently utilizes rocks and other ground cover as winter retreats (Robb 1980b). Max-

imum SVL is 85 mm (Robb 1980a). Mating in captivity occurs in September or October and young are born in late Autumn (April—May) (Robb 1980b; Rowlands 1981a). Robb (1980a, 1980b) describes threat posturing and barking in the male.

Naultinus rudis (Fischer, 1882) (Fig. 54)

1882 *Heteropholis rudis* Fischer. Abh.Naturwiss.Ver. Bremen 7: 236; pl. 16, figs. 1—5.
Type locality: Neuseeland.
Holotype: BMNH 1946.8.22.37.
1885 *Naultinus rudis* Boulenger. Catalogue of Lizards in the British Museum, vol. 1: 170.
1955 *Heteropholis rudis* McCann. Dominion Mus.Bull. 17: 57; pls. 4 (figs. 1—6), 4,5.
1982 *Naultinus elegans rudis* Meads. New Zealand Herpetology: 324.
1982 *Naultinus rudis* (part) Thomas. New Zealand Herpetology: 336.
1986 *Naultinus elegans rudis* Gill. Collins Handguide to the Frogs and Reptiles of New Zealand: 48.

D i a g n o s i s : Two ribless cervical vertebrae; five—six abdominal ribs; rostral contacts nostril; dorsal scalation heterogeneous, entire body covered with irregular conical scales. (33, 79).

Fig.54: Holotype of *Heteropholis rudis* Fischer, 1882 (= *Naultinus rudis*). BMNH 1946.8.22.37. (Photo courtesy of British Museum (Natural History))

C o m m e n t s : Fischer's (1882) description is detailed and accurate. Thomas (1982a) suggested synonymizing *N. manukanus* with *N. rudis* and described variation throughout the range of the two taxa. *Naultinus rudis* is distributed in patches in the northeastern part of the South Island in parts of Nelson, Marlborough and Canterbury (Fig. 51). In the Kaikoura Ranges it occurs at elevations of up to 400 m (Robb 1980b) and is most often found in manuka or kanuka (Werner & Whitaker 1978), although it has also been reported from a variety of other plants including *Pseudopanax* (Robb 1980b). Maximum size is 72 mm SVL (NMNZ G855). Mating takes place in September—October (June—October in captivity) and young are born in March or April (Robb 1980b; Rowlands 1981a).

Naultinus stellatus Hutton, 1872 (Fig. 55)

1872 *Naultinus elegans stellatus* Hutton. Trans.Proc. New Zealand Inst. (1871) 4:(171). Type locality: Lake Rotoiti, Nelson District, South Island, New Zealand (type locality of Hutton 1872 = near the top of Mount Arthur, New Zealand).
Holotype: MNNZ (specimen "not available" fide McCann 1955).
Neotype: NMNZ R458.

Fig.55: *Naultinus stellatus* male from Station Creek, Upper Buller Valley, South Island, New Zealand. SVL = 75 mm. (Photo courtesy of B.W. Thomas)

1877 *Naultinus pulcherrimus* Buller. Trans.Proc. New Zealand Inst. 9: 326; pl. 17 top and middle.

Type locality: One of the Nelson and Foxhill railway stations, in the Waimea District, South Island, New Zealand.

Holotype: NMNZ (specimen "not available" fide McCann 1955).

1955 *Hetropholis stellatus* McCann. Dominion Mus.Bull. 17: 66; pl. 7 (figs. 1—7).

1982 *Naultinus elegans stellatus* Meads. New Zealand Herpetology: 324.

1982 *Naultinus stellatus* Thomas. New Zealand Herpetology: 336.

1986 *Naultinus elegans stellatus* Gill. Collins Handguide to the Frogs and Reptiles of New Zealand: 48.

D i a g n o s i s : Lumbar vertebrae generally two; dorsal scalation of head and nape heterogeneous, granular; supraciliary scales granular.

C o m m e n t s : *Naultinus stellatus* is distributed through the Nelson Lakes district and in the Maitai Valley in Nelson Province (Fig. 51). Mainwaring (1979) and Robb (1980b) described geographical variation in the species. Specimens have been found on red beech (Robb 1980b) as well as *Coprosma* and *Rubus* at a height of 1.2 to 1.5 m (Werner & Whitaker 1978). Hutton (1872) reports finding a specimen under a stone in the snow on Mt. Arthur. Maximum size is 79 mm SVL (UMMZ 132102). There is a distinct reduction of activity in winter (May—July) (Mainwaring 1979; Robb 1980b). Mating occurs in late winter or spring and young are born in autumn or early winter (Robb 1980b; Rowlands 1979, 1981a). Rowlands (1981b) reports blowfly *(Calliphora)* infestations in *N. stellatus* in captivity. Buller (1877) described a tail-coiling behavior.

Naultinus tuberculatus (McCann, 1955)

1955 *Heteropholis tuberculatus* McCann. Dominion Mus.Bull. 17: 61.

Type locality: Westland, South Island.

Holotype: CMC (specimen number unknown).

1982 *Naultinus elegans tuberculatus* Meads. New Zealand Herpetology: 324.

1982 *Naultinus tuberculatus* Thomas. New Zealand Herpetology: 336.

1986 *Naultinus elegans tuberculatus* Gill. Collins Handguide to the Frogs and Reptiles of New Zealand: 48.

D i a g n o s i s : Dorsal scales of head and nape heterogeneous, conical, flattened; rostral contacts nostril. (79).

C o m m e n t s : *Naultinus tuberculatus* occurs in the extreme northwestern parts of the South Island in parts of Nelson Province and Westland (Fig. 51). It reaches a maximum size of 77 mm SVL (McCann 1955). This species, found in manuka and kanuka (Robb 1980b), feeds on moths, flies and other invertebrates (Robb 1980b). Mating occurs in September—October and young are born in March—May (Robb 1980b; Rowlands 1981a). Robb (1980b) described male aggressiveness.

Nephrurus Günther, 1876

1876 *Nephrurus* Günther. J.Mus. Godeffroy 5: 46.
Type species: *Nephrurus asper* Günther 1876 by monotypy.
1965 *Underwoodisaurus* Wermuth. Das Tierreich 80: IX (nomen substitutum pro *Phyllurus* Schinz, 1822 (part)).

S p e c i e s r e f e r r e d : *Nephrurus asper* Günther, 1876; *N. deleani* Harvey, 1983; *N. laevissimus* Mertens, 1958; *N. levis* De Vis, 1886; *N. milii* (Bory de Saint-Vincent, 1825); *N. sphyrurus* (Ogilby, 1892); *N. stellatus* Storr, 1968; *N. vertebralis* Storr, 1963; *N. wheeleri* Loveridge, 1932.

D i a g n o s i s : Node 3 (Fig. 17) corresponds to a monophyletic taxon including the knob-tailed species of *Nephrurus* and the two species of *Nephrurus* formerly assigned to the genus *Phyllurus*, *N. milii* and *N. sphyrurus*. This grouping is diagnosed by the following characters: zero or one inscriptional ribs; sternum short and narrow; clavicular fenestrae very large; head large; skin bearing rosettes around tubercles; digits generally short; regenerated tail short and bulbous. (32-A, 34*, 43*, 81, 98*).

Within the genus a further monophyletic grouping (Node 4) exists, uniting the species *N. asper, deleani, laevissimus, levis, stellatus, vertebralis* and *wheeleri*. This node, corresponding to the knob-tailed *Nephrurus*, is diagnosed by the following characters: frontal bone approximately as wide as long; caudal vertebrae fewer than 30; coracoid processes of interclavicle indistinct; phalangeal formula reduced; hypoischium extending posteriorly to the level of the vent; metatarsal length (shortest to longest) V-I-IV-III-II; metatarsals I—IV greater than two times length of longest respective phalanges; digit V of pes offset from others; dorsal color pattern of three dark bands on head, nape and shoulders; ventral toe scalation spinose; claws slender at base, slightly decurved; labial scales only slightly larger than neighboring scales; cartilagenous rod of regenerated tail lacking or amorphous; tail terminating in a small knob. (4*, 25, 40, 46*, 51*, 55*, 56, 61, 71*, 77*, 85*, 99*, 100).

C o m m e n t s : Because the distribution of *Nephrurus* is chiefly to the west of the Great Dividing Range in the more arid regions of the Australian continent, many of the species have only recently been described. Keys for the species are provided by Cogger (1986) but rely on variable characters. Storr (1963) provided a phenetic catalogue and key to the Western Australian species. Delean (1982) gave diagnoses and descriptions for the species of South Australia and the Northern Territory and also provides notes on biology. Cogger et al. (1983) presented a partial synonymy of all species as well as a summary of distribution and habitat.

Pianka & Pianka (1976) presented detailed findings on the ecology of three Western Australian species *(N. laevissimus, levis* and *vertebralis)*. Members of the genus are entirely terrestrial. The knob-tailed species burrow or utilize the burrows of other animals as daytime refuges. The odd tail may be used in thermoregulation and/or monitoring mechanical stimuli (Russell & Bauer 1988). Most are associated with sandplains or sandridges, although *N. asper* uses a broader range of habitats and *N. milii* and especially *N. sphyrurus* are typically associated with more mesic habitats. Barrett (1950) reported
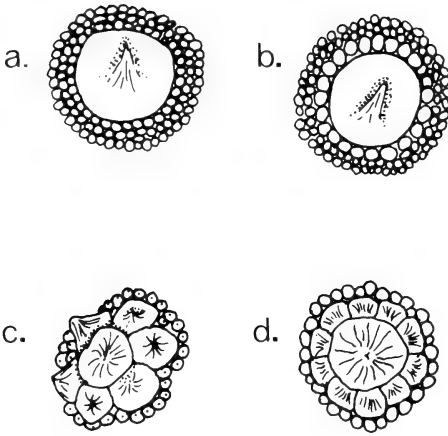
Fig.56: Dorsal body tubercles of (a) *Nephrurus deleani*, (b) *N. stellatus*, (c) *N. asper*, (d) *N. wheeleri* (see *Nephrurus* key couplet 3) (a and b redrawn from Harvey 1983).

the occurrence of unspecified *Nephrurus* in caves and mines. All species lay two eggs and feed primarily on a variety of arthropods and small nocturnal vertebrates (mostly other geckos).

Key to the Species of *Nephrurus*

1a. Subdigital surface lamellate 2
b. Subdigital surface spinose 3
2a. Anterior loreals minute .... *N. milii*
b. Anterior loreals only slightly smaller than posterior .... *N. sphyrurus*
3a. Entire dorsum covered by sets of conical scales surrounded by rosettes of smaller conical scales (Fig. 56) 4
b. Body without conical tubercles and rosettes 5
4a. 8 interorbital scales, preocular scales not enlarged .... *N. asper*
b. 6 or fewer interorbital scales, vertical series of enlarged, tubercular preocular scales .... *N. wheeleri*
5a. Flanks (and most of dorsum) smooth .... *N. laevissimus*
b. Flanks and dorsum with scattered small tubercles 6
6a. Anterior face of forearm with scattered, enlarged conical tubercles ($\approx$ 2x neighboring scales) (Fig. 57) 7
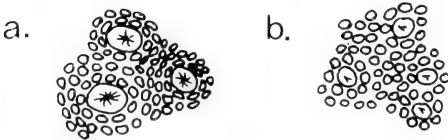b. Anterior face of forearm with small, flattened tubercles 8

Fig.57: Scalation of the anterior face of the forearm of (a) *Nephrurus levis* and (b) *N. stellatus* showing relative size of tubercles (*Nephrurus* key couplet 6).

7a. Mental rectangular, posterior dorsal tubercles surrounded by rosettes of slightly enlarged scales .... *N. deleani*

b. Mental hemispherical, scales of rosettes not enlarged .... *N. stellatus*

8a. Skin of ventral surface of articular region of jaw with scattered, enlarged tubercles .... *N. levis*

b. Skin of ventral surface of articular region of jaw with few or no enlarged tubercles .... *N. vertebralis*

Nephrurus asper **Günther, 1876 (Fig. 58)**

1876 *Nephrurus asper* Günther. J.Mus. Godeffroy 5: 46.
Type locality: Peak Downs, Queensland.
Holotype: BMNH 1946.8.23.34.

D i a g n o s i s : Dorsal skin of head co-ossified with skull; posterior border of parietals complete; roofing entire occipital region; squamosal large and broad; metatarsals I—IV one and a half or fewer times the length of corresponding phalanges; phalangeal formulae 2-3-4-4-3 (manus), 2-3-4-4-4 (pes); dorsal pattern of head and nape without three dark bands; eight or more interorbital scales; preocular sclaes not enlarged; rosettes around dorsal tubercles spinose; anterior loreal scales minute; tail extremely short; 4—5 longitudinal rows of caudal tubercles; 8—12 caudal annuli. (1, 7, 11, **56, 61**, 83-B, 87).

C o m m e n t s : This is the largest species in the genus (maximum SVL 136 mm, AMS R104458) (McPhee 1979 attributed the unlikely total length of 200 mm to this species).
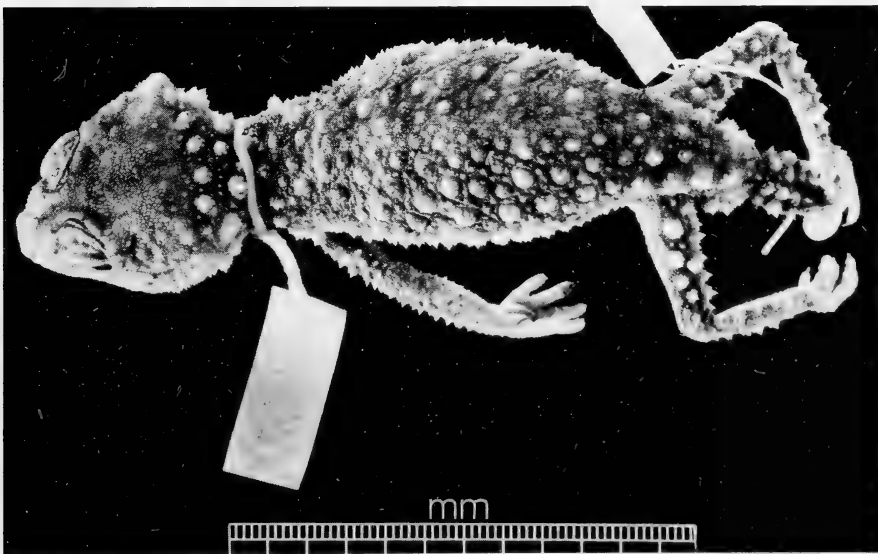

Fig.58: Holotype of *Nephrurus asper* Günther, 1876. BMNH 1946.8.23.34. (Photo courtesy of British Museum (Natural History))

For some reason much confusion seems to have surrounded the size and distribution of this species. For example, Worrell (1963) gives inland Queensland for the range and lists this species size as being second in diminutiveness only to *N. laevissimus*. Specimens from the south-central Northern Territory appear to attain larger sizes than those in other parts of the range.

Nephrurus asper ranges across most of northern Australia from the Kimberleys to the central Queensland coast and as far south as the South Australian border and south-central Queensland. In the Northern Territory it ranges from the arid regions of the central desert to the moist tropical rock outcrops of the Alligator Rivers drainages (Fig. 59). The ecology of *N. asper* is atypical for the genus as a whole. It occurs in rocky areas and may excavate burrows under logs, rocks, bark or other debris (Delean 1982). In Arnhem Land (N.T.), it is found in association with sandstone caves, cliffs and outcrops (Cogger 1981). Longman (1918), Bustard (1967b) and Gow (1979) have reported on the typical defensive behavior and vocalization of this species and Gow (1979) documented aspects of egg-laying and burrowing. There are no autotomy septa in *N. asper* — an autapomorphy for this taxon. The natural diet of the species includes small insects and spiders (Broom 1897; Gow 1979). Skinks are also taken in captivity and it is likely that small lizards in general may be important prey items.
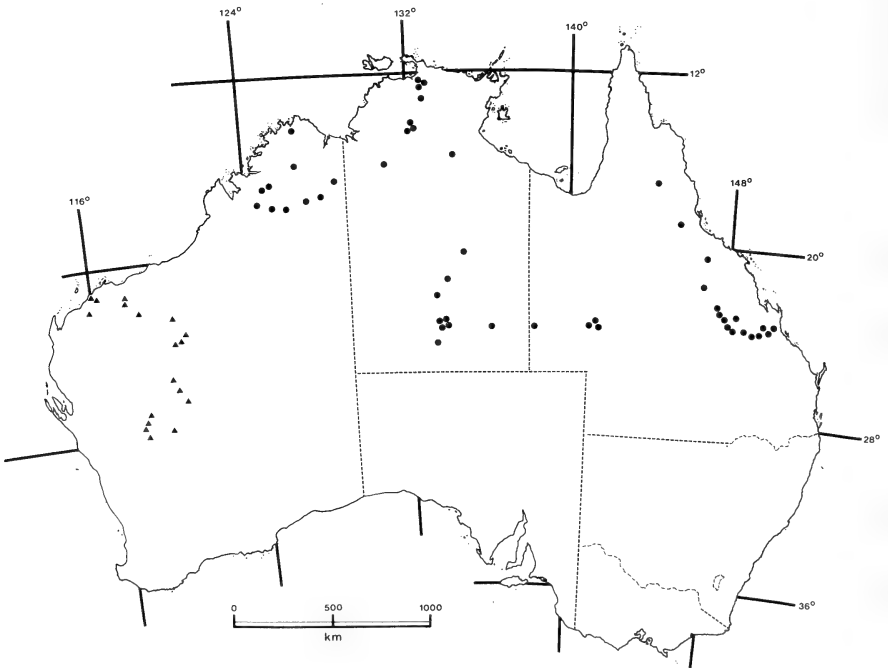

Fig.59: Distribution of *Nephrurus asper* (circles) and *N. wheeleri* (triangles) in Australia.

Nephrurus deleani **Harvey, 1983 (Fig. 60)**

1979 *Nephrurus vertebralis* (part) Cogger. Reptiles and Amphibians of Australia, 2nd ed.: 166.

1983 *Nephrurus deleani* Harvey. Trans.Roy.Soc.S.Aust. 107: 232; figs. 2,3.

Type locality: 44 km SE of Pimba, South Australia (31°31'S 137°08'E).

Holotype: SAMA R21868.

D i a g n o s i s : Single lumbar vertebra; phalangeal formulae 2-3-3-3-3 (manus and pes); metatarsals two or more times length of corresponding phalanges; anterior face of forelimb with scattered enlarged conical tubercles; flanks with scattered tubercles;

Fig.60: Holotype of *Nephrurus deleani* Harvey, 1983. SAMA R21868. SVL 79.3 mm. (Photo courtesy of South Australian Museum)
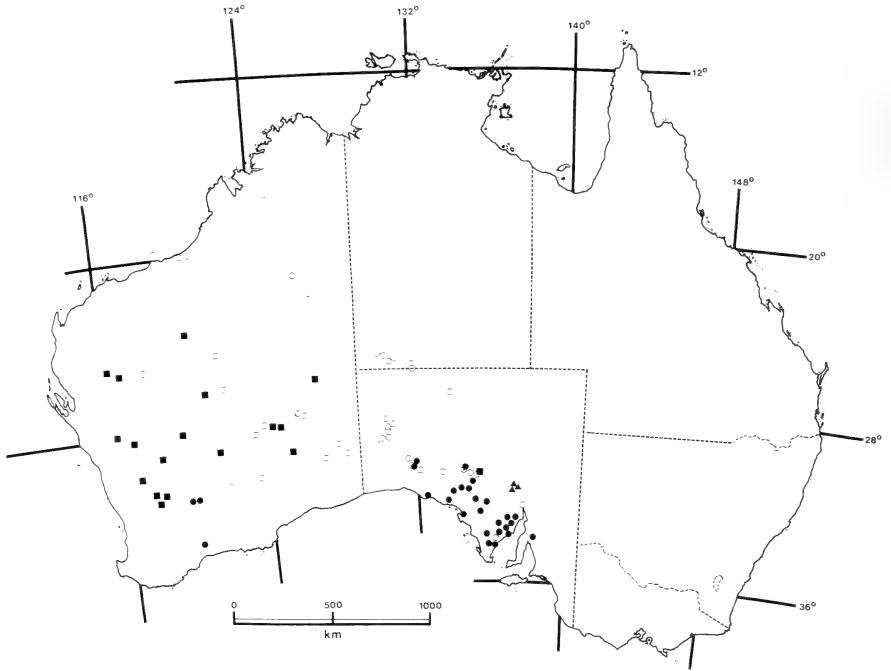
144

Fig.61: Distribution of *Nephrurus deleani* (closed triangles), *N. laevissimus* (open circles), *N. stellatus* (closed circles) and *N. vertebralis* (closed squares) in Australia.

mental rectangular; posterior dorsal tubercles surrounded by rosettes of slightly enlarg-ed scales; tail moderate, with 9—10 rows of tubercles and 15—17 caudal annuli. (23).

C o m m e n t s : This species, first discovered in 1971, was believed to represent a dis-junct population of *N. vertebralis*, otherwise known only from Western Australia. The type description of Harvey (1983) is detailed and useful. Maximum size recorded for *N. deleani* is 98 mm SVL (Delean 1982). As in all its congeners, females are generally larger than males. Maturity is reached at about 55 mm (Delean 1982). The species is endemic to the region of Pernatty Lagoon in south-central South Australia (Figs. 61,62). It is associated with the sand hills to the north and west of the lagoon (a dry salt lake bed) which are dominated by *Acacia aneura* and *A. ligulata* (Harvey 1983). Surrounding salt lakes and the Gawler Ranges to the south west apparently present a barrier to contact with *N. levis* and *N. laevissimus* (Harvey 1983). *Nephrurus deleani* inhabits the crests of red dunes in this area of low rainfall (< 175 mm/yr) and feeds on moths, spiders, scorpions and several sympatric geckos *(Diplodactylus damaeus, Gehyra variegata* and *Rhynchoedura ornata)* as well as other small nocturnal animals (Delean 1982). Delean (1982) presented additional information on population structure, tail-break frequency and behavior (including a description of scorpion feeding in this species).

Fig.62: Red sand desert with dry lake in background right, vicinity of Birthday, South Australia — near region of greatest sympatry or near-sympatry of species of *Nephrurus*.

Nephrurus laevissimus **Mertens, 1958**

1924 *Nephrurus levis* (part) Kinghorn. Rec.Aust.Mus. 14: 166.
1958 *Nephrurus laevissimus* Mertens. Senckenberg.Biol. 39: 51; pl. 3 (fig. 4).
Type locality: Dünen etwa 2 km NW des Ayers Rock, Northern Territory, Zentral-Australien.
Holotype: SMF 53201.

D i a g n o s i s : Two ribless cervical vertebrae; phalangeal formulae 2-3-3-3-3 (manus and pes); metatarsals two or more times length of corresponding phalanges; flanks smooth; tail moderate, with 5—7 rows of caudal tubercles and 13—19 caudal annuli.

C o m m e n t s : Mertens' (1958) description is adequate. *Nephrurus laevissimus* occurs in sandridge regions throughout the arid zone (Fig. 61) and is in sympatry with *N. asper* in the southern Northern Territory, with *N. levis* across northern South Australia, with *N. vertebralis* in eastern Western Australia and with *N. stellatus* in a narrow band across the Nularbor Plain. It reaches a maximum SVL of 87 mm (Delean & Harvey 1981). Pianka & Pianka (1976) and Delean & Harvey (1981), in Western and South Australia respectively, found *N. laevissimus* in association with *Triodia* dominated sandridges where populations may be locally very dense. It feeds primarily on spiders, coleopterans

and a variety of other arthropods, and on the diplodactyline gecko *Rhynchoedura ornata* (Pianka & Pianka 1976). Delean & Harvey (1981) provided further information on population structure and Pianka & Pianka (1976) gave a detailed analysis of diet, activity period, temperatures and morphometrics. Tail break frequencies in this species are the lowest known for any autotomizing gecko (0.6%) (Pianka & Pianka 1976). Jones (1985) recorded nematode parasites.

Nephrurus levis De Vis, 1886 (Fig. 63)

1886 *Nephrurus levis* De Vis. Proc.Linn.Soc. New South Wales (2)1: 168.
Type locality: not given (Chinchilla, SE Queensland — fide Covacevich 1971).
Holotype: QM J246.
1886 *Nephrurus platyurus* Boulenger. Ann.Mag.Nat.Hist. (5)18: 91.
Type locality: Adelaide, South Australia.
Holotype: BMNH 1946.8.23.42.
1887 *Nephrurus laevis* Boulenger. Catalogue of Lizards in the British Museum (Natural History), vol. 3: 477 (nomen emendatum pro *Nephrurus levis* De Vis, 1886).
1910 *Nephrurus platyurus* Werner. Die Fauna Südwest-Australiens II: 451.
1929 *Nephrurus levis* Waite. The Reptiles and Amphibians of South Australia: 69; fig. 36.
1961 *Nephrurus laevis* Glauert. A Handbook of the Lizards of Western Australia: 10; fig. 3(2).
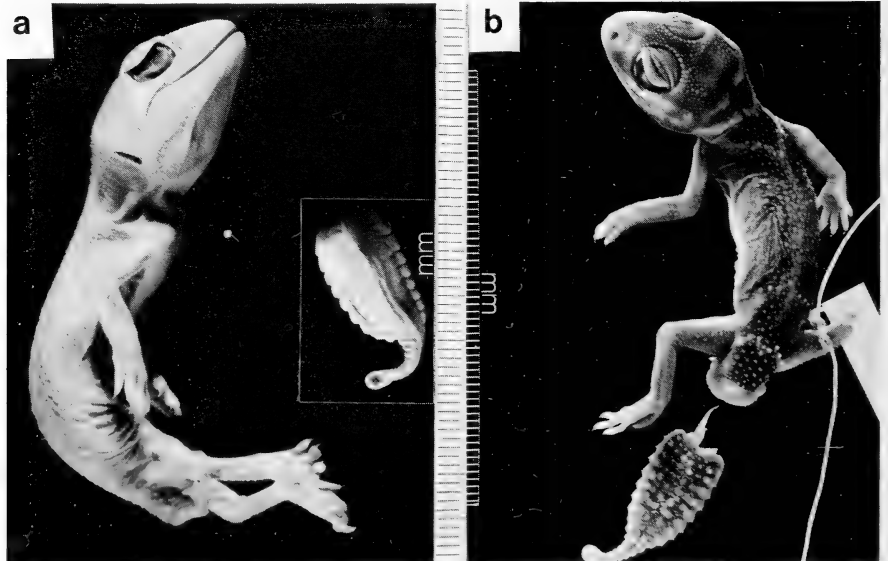

Fig.63: a. Holotype of *Nephrurus levis* De Vis, 1886. QM J246. (Photo courtesy of Jeanette Covacevich, Queensland Museum) b. Holotype of *Nephrurus platyurus* Boulenger, 1886 (= *Nephrurus levis*). BMNH 1946.8.23.42. (Photo courtesy British Museum (Natural History))

1963 *Nephrurus levis levis* Storr. J.Roy.Soc.W.Aust. 46: 87; fig. 2, middle right.
1963 *Nephrurus levis occidentalis* Storr. Ibid.: 88.
Type locality: Narryer, Western Australia, (26°34'S, 115°56'E).
Holotype: WAM R13918.
1963 *Nephrurus levis pilbarensis* Storr. Ibid.: 88.
Type locality: 12 miles E of Mundabullangana, Western Australia, (20°31'S, 118°13'E).
Holotype: WAM R14835.
1970 *Nephrurus laevis* Davey. Australian Lizards: 35.
1975 *Nephrurus levis* Cogger. Amphibians and Reptiles of Australia: 165; figs. 75,408.

D i a g n o s i s : Skin of head co-ossified with skull; posterior border of parietal complete; 30 or more caudal vertebrae; metatarsals two or more times longer than corresponding phalanges; phalangeal formulae 2-3-3-3-3 (manus and pes); anterior loreal scales minute; flanks and dorsum with small scattered tubercles; anterior face of forelimb with small flattened tubercles; skin of ventral surface of articular region of jaw with scattered, enlarged tubercles; tail long, broad, with 6—10 rows of caudal tubercles and 12—21 caudal annuli. (1, 7, **25**, 87).

C o m m e n t s : De Vis (1886) provided an excellent decription of this species. Systematic confusion has occasionally resulted from the inclusion of other taxa into this taxon and there have been repeated shifts in the spelling of the specific epithet as zoologists trained in Latin have unconsciously rectified De Vis's spelling error. *Nephrurus levis* is the most widespread and variable member of the genus. Its range includes most of arid and semi-arid central Australia west from the Great Dividing Range to the coast of central Western Australia (Fig. 64). *Nephrurus levis* is common both on inland red dunes and coastal white dunes in the regions of Shark Bay (Storr & Harold 1978) and Exmouth (Storr & Hanlon 1980), but rarer near Geraldton to the south (Storr et al. 1983). In the Western Australian wheatbelt *N. levis* occurs exclusively on sandy loams in shrubland (Chapman & Dell 1985). It has also been recorded from Bernier, Dorre and Dirk Hartog Islands near the Peron Peninsula (Storr & Harold 1978). It occurs in all mainland states except Victoria. Storr (1963) divided this species into three subspecific forms in Western Australia.

The maximum known SVL is 94 mm (Waite 1929), Swanson (1976) credits this species with a total length of up to 150 mm. Like most of its congeners it burrows in areas of sandy soil associated with *Triodia*. It feeds on a very wide range of arthropods (especially spiders, beetles, locusts and scorpions) as well as *Rhynchoedura ornata* (Pianka & Pianka 1976). Waite (1929) cited the association of this species with logs and stones but this would appear to be an atypical habitat and, like his description of defensive behavior, be in reference to *N. asper*. Like all diplodactylines it lays two eggs. A photograph by Greer (1981) illustrates a mating pair of *N. levis* with the smaller male biting the nape of the female as he mounts. My observations condtradict Bustard's (1967b) claim that this species does not exhibit a defensive display. Pianka & Pianka (1976) gave detailed information on many aspects of the ecology of this species. Heatwole (1976) reports a particular resistance to cold in this taxon.
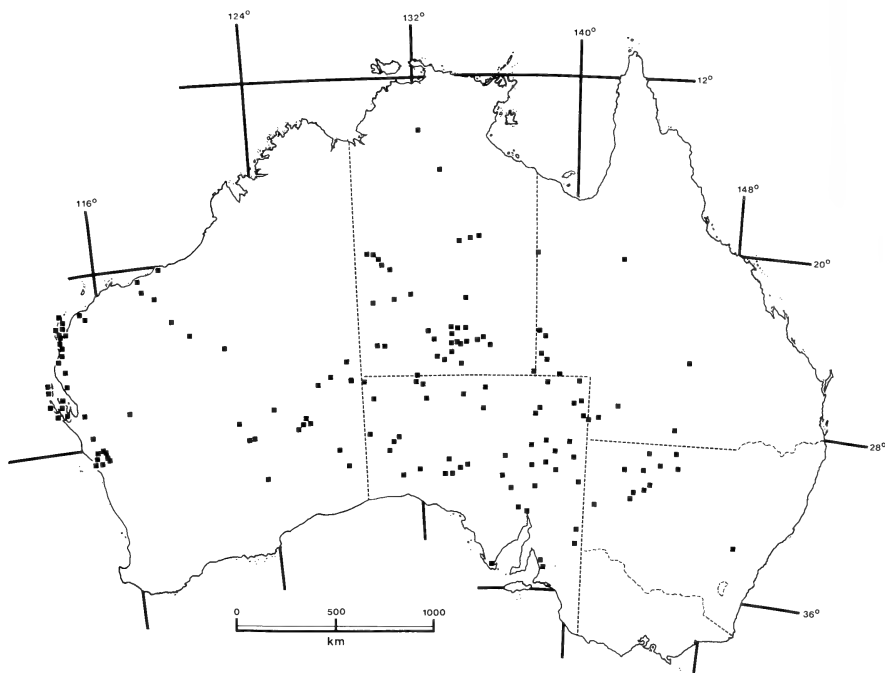
Fig.64: Distribution of *Nephrurus levis* in Australia.

Nephrurus milii (Bory de Saint-Vincent, 1825) (Fig. 65)

1825 *Phyllurus milii* Bory de Saint-Vincent. Dictionnaire Classique d'Histoire Naturelle, vol. 7: 183.

Type locality: Rives de la baie des Chiens-Marins, Australasie (= Shark Bay, Western Australia).

Holotype: presumed lost.

1831 *Cyrtodactylus milii* Gray. The Animal Kingdom Arranged in Conformity with its Organization by the Baron Cuvier, vol. 9: 52 (lapsus pro *Phyllurus milii* Bory de Saint-Vincent, 1825).

1836 *Gymnodactylus miliusii* Duméril & Bibron. Erpétologie Générale, vol. 3: 430; pl. 33 (fig. 1) (nomen substitutum pro *Phyllurus milii* Bory de Saint-Vincent, 1825).

1843 *Gymnodactylus (Anomalurus) miliusii* Fitzinger. Systema Reptilium: 90.

1845 *Phyllurus miliusii* Gray. Catalogue of the Specimens of Lizards in the Collection of the British Museum: 176.

1857 *Gymnodactylus vittatus* Anonymous. Storia Naturale Illustrata del Regno Animale, vol. 3: 61; fig. 2160 (lapsus pro *Gymnodactylus miliusii* ad Duméril & Bibron, 1836; non *Gymnodactylus vitattus* Lichtenstein, 1856).

1867 *Phyllurus myliusii* Gray. The Lizards of Australia and New Zealand in the Collection of the British Museum: 6; pl. 17 (fig. 2) (ex errore pro *Phyllurus miliusii* ad Duméril & Bibron, 1836).

1885 *Gymnodactylus miliusii* Boulenger. Catalogue of the Lizards in the British Museum, vol.1: 48.

1913 *Gymnodactylus asper* Boulenger. Ann.Mag.Nat.Hist. (8)12: 563.

Type locality: Milparinha (= Milparinka), western New South Wales.

Holotype: BMNH 1913.7.28.1.

1934 *Gymnodactylus milii* Loveridge. Bull.Mus.Comp.Zool. 77: 299.

1950 *Gymnodactylus milusii* Barrett. Reptiles of Australia: 30 (ex errore pro *Phyllurus miliusii* ad Duméril & Bibron, 1836).

1954 *Phyllurus milii* Underwood. Proc.Zool.Soc. London 124: 474.

1961 *Gymnodactylus milii* Glauert. A Handbook of the Lizards of Western Australia: 12; fig. 3(5).

1964 *Phyllurus miliusii* Dixon & Kluge. Copeia 1964: 180.

1965 *Gymnodactylus (Underwoodisaurus) milii* Wermuth. Das Tierreich 80: IX.

1967 *Phyllurus milii* Kluge. Aust.J.Zool. 15: 1017.

1967 *Gymnodactylus milii* Cogger. Australian Reptiles in Colour: 25; pl. 8.

1967 *Phyllurus mili* Bustard. Herpetologica 23: 128.

1970 *Underwoodisaurus milii* Bustard. Australian Lizards: 58; pl. 27.

1978 *Phyllurus milii* Storr & Harold. Rec.West.Aust.Mus. 6: 455.

1979 *Underwoodisaurus milii* Cogger. Reptiles and Amphibians of Australia, revised (2nd) ed: 178.

1980 *Phyllurus milii* Russell. J.Herpetol. 14: 415.

1983 *Phyllurus milii* Storr et al. Rec.West.Aust.Mus. 10: 221.
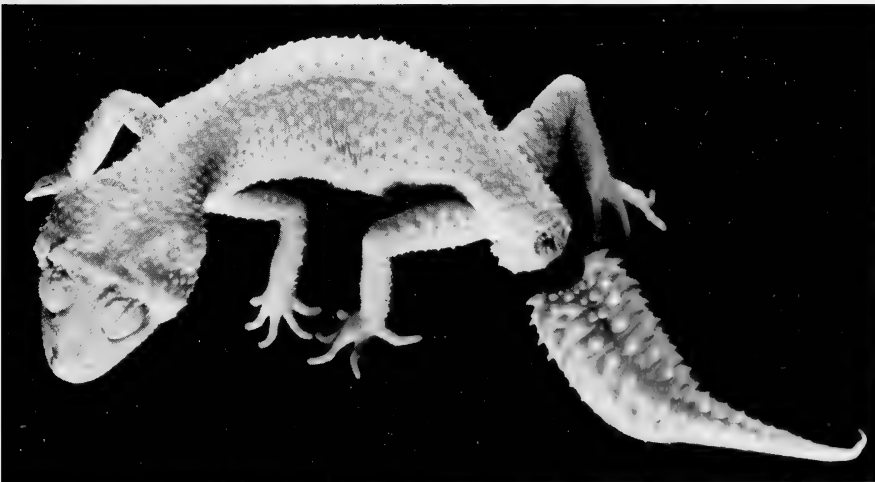

Fig.65: *Gymnodactylus asper* Boulenger, 1913 (= *Nephrurus milii*). BMNH 1913.7.28.1. SVL = 105 mm. (Photo courtesy of British Museum (Natural History))

1983 *Underwoodisaurus milii* Cogger. Reptiles and Amphibians of Australia, 3rd ed: 198; fig. 479.
1987 *Phyllurus milii* King. Aust.J.Zool. 35: 510.

D i a g n o s i s : Trunk vertebrae "procoelous"; anterior loreal scales minute; postmental scales enlarged anteriorly; digits with subdigital lamellae; tail elongate; phalangeal formula unreduced; dorsal pattern of three bands on head and nape absent; labial scales much larger than neighboring scales; claws deep, recurved; no terminal knob on tail. (21, **81**, 87).

C o m m e n t s : The placement of this species has, in the past, been the major instability in the composition of *Phyllurus*, to which it appears only distantly related. Otherwise there has been little confusion over the identity of this gecko, although at least five different spellings of its specific epithet have been employed. Bory de Saint-Vincent (1825) described an animal from the north-western extreme of the range. Although incomplete, it is sufficient to identify the species without question. *Gymnodactylus asper* Boulenger, 1913 is an extremely large (105 mm SVL), faded *N. milii* with a regenerated tail. An anonymous (1857) Italian distillation of Duméril & Bibron (1836) inexplicably uses the name *Gymnodactylus vittatus* for this species, but this is definitely an error in copying rather than an attempted revision of the specific epithet.

Maximum total lengths of 200 mm have been reported (McPhee 1979) but are probably extremely rare. Specimens from western New South Wales and some offshore islands (Bush 1981) tend to be larger than those from elsewhere in the range, which includes extreme southern Queensland, most of New South Wales and northern Victoria and sweeps across South and Western Australia, intermittantly penetrating several hundred miles inland (Fig. 66). Two records from Northern Queensland are probably in error although there are two reliable records from the southern part of the Northern Territory (Strong & Gillam 1983; R.W. Murphy pers. comm.). North of Perth, *N. milii* is restricted to a narrow coastal belt stretching almost as far north as Exmouth. A single specimen is recorded from Onslow. *Nephrurus milii* is widely distributed on islands off the west and south coasts of the continent, including Bernier, Dorre and Dirk Hartog Islands (near Shark Bay, W.A.) (Storr & Harold 1978), the Houtman Abrolhos (Alexander 1921; Loveridge 1934; Storr et al. 1983) Kangaroo and St. Francis Islands (Waite 1929), Franklin Islands (Schwaner 1985) and the Recherche Archipelago (Kinghorn 1924; Bush 1981).

In coastal Western Australia *Nephrurus milii* is found in association with limestone caves and cliffs (Storr & Harold 1978; Storr et al. 1983). Barrett (1950) refers to this terrestrial species as a house gecko, although this, in the standard use of the phrase, is incorrect. In the eastern parts of its range *N. milii* is known from red sand plains, mallee heath and sclerophyll forest in granite, sandstone and limestone areas (Wells & Wellington 1984). In the Western Australian wheatbelt it is primarily associated with rocky outcrops and woodlands (Chapman & Dell 1985). Over most of its range it is found during the day under logs, rocks and other debris and among exfoliating granite outcrops. Swanson (1976) states that it may also be found in burrows. Communal egg-laying (McPhee 1979; pers. obs.) and over-wintering aggregations in rock crevices (Wells
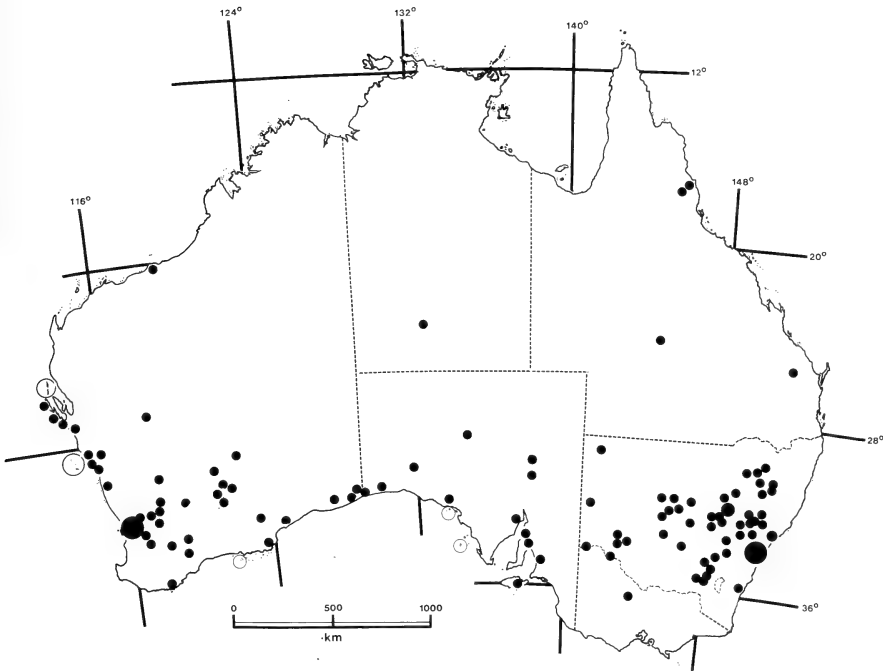
Fig.66: Distribution of *Nephrurus milii* in Australia. Large circles represent 5 or 10 (largest circles) localities in close proximity.

& Wellington 1983) have been reported. Defensive behavior (Bustard 1967b) and tail autotomy and function (Waite 1929) have been considered. Diet includes small lizards (McPhee 1979) as well as many insects and arachnids. *Nephrurus milii* is known to be prey to tiger snakes *Notechis ater niger* (Schwaner 1985) and feral cats (Strong & Gillam 1983).

Nephrurus sphyrurus **(Ogilby, 1892) (Fig. 67)**

1892 *Gymnodactylus sphyrurus* Ogilby. Rec.Aust.Mus. 2: 6.
Type locality: interior of New South Wales (Tumut? — sic!).
Holotype: AMS R3800.
1931 *Heteronota walshi* Kinghorn. Rec.Aust.Mus. 18: 268; fig. 2.
Type locality: Boggabri, on the northern tablelands of New South Wales.
Holotype: AMS R10266.
1965 *Gymnodactylus sphyrurus* Wermuth. Das Tierreich 80: 67.
1967 *Phyllurus sphyrurus* Kluge. Aust.J.Zool. 15: 1017.
1975 *Underwoodisaurus sphyrurus* Cogger. Reptiles and Amphibians of Australia: 179; fig. 80.
1980 *Phyllurus sphyrurus* Russell. J. Herpetol. 14: 415.

1983 *Underwoodisaurus sphyrurus* Cogger. Reptiles and Amphibians of Australia, 3rd ed: 198; fig. 88.

D i a g n o s i s : Caudal vertebrae fewer than 30; post-pygal pleurapophyses well developed; no enlarged post-mental scales; anterior loreal only slightly smaller than posterior; tail short, very wide, without knob at terminus; non-scansorial subdigital lamellae present; phalangeal formula unreduced; without dorsal patterns of three dark bands on head and nape. (25, **27**, 81).

Fig.67: a. Holotype of *Gymnodactylus sphyrurus* Ogilby, 1892 (= *Nephrurus sphyrurus*). AMS R3800. b. Holotype of *Heteronota walshi* Kinghorn, 1931 (= *Nephrurus sphyrurus*). AMS R10266. (Photos courtesy of The Australian Museum)

C o m m e n t s : Ogilby's (1892) description is adequate, but not completely useful for differentiating all specimens of this species from *N. milii*, with which he suggested close alliance. Kinghorn (1931) placed a specimen from Boggabri, N.S.W. in the genus *Heteronota (= Heteronotia)*. Maximum SVL is 81 mm (AMS R4880). Little is known of the ecology of this species. It is known only from the cool granitic highland areas of the Murray-Darling Basin (Fig. 72). Czechura & Covacevich (1985) considered this species to be at indeterminate risk owing to its patchy distribution in an area of great human impact.

Nephrurus stellatus **Storr, 1968**

1968 *Nephrurus stellatus* Storr. W.Aust.Nat. 10: 180; fig. 1.
Type locality: 41 miles E of Southern Cross, Western Australia, (31°25'S, 120°00'E).
Holotype: WAM R28363.

D i a g n o s i s : Two ribless cervical vertebrae; lumbar vertebrae two in number; metatarsal two or more times length of corresponding phalanges; phalangeal formulae 2-3-3-3-3 (manus and pes); flanks and dorsum with scattered small tubercles; anterior face of forelimb with scattered, enlarged conical tubercles; mental hemispherical; rosette scales not enlarged; dorsal pattern of distinct white spots; tail moderate, with 5—7 caudal tubercle rows, 9—14 caudal annuli.

C o m m e n t s : *Nephrurus stellatus* is distributed in a narrow belt across the southern part of Australia from the Eyre Peninsula to central Western Australia (Fig. 61). It reaches a maximum size of 84 mm SVL (Delean 1982). This species is associated with sandy soils dominated by *Eucalyptus* and *Triodia* (Delean 1982) or *Eucalyptus* and *Maleleuca* (Galliford 1981). Burrows are often constructed at the base of *Triodia* bushes. The diet consists of small nocturnal arthropods and perhaps other geckos.

Nephrurus vertebralis **Storr, 1963**

1961 *Nephrurus laevis* (form 2) Glauert. A Handbook of the Lizards of Western Australia: 10.
1963 *Nephrurus vertebralis* Storr. J.Roy.Soc.W.Aust. 46: 88; fig. 2 top right.
Type locality: Jibberding, Western Australia (29°58'S, 116°51'E).
Holotype: WAM R5231.

D i a g n o s i s : Scleral ossicles fewer than 30; caudal vertebrae greater than 30 in number; metatarsals two or more times length of corresponding phalanges; phalangeal formulae 2-3-3-3-3 (manus and pes); flanks and dorsum with small scattered tubercles, anterior face of forearm with small, flattened tubercles, ventral surface of articular region of jaw smooth, white mid-dorsal stripe extending on to tail; tail moderate, with 7—8 rows of caudal tubercles, 17—19 caudal annuli. (15, **25**).

C o m m e n t s : This species reaches a maximum SVL of 92 mm (Storr 1963) and is distributed throughout the central portion of Western Australia as far south as the northeastern Wheat Belt (Fig. 61). Storr's (1963) description is largely uninformative. Pianka & Pianka (1976) reported that the species is associated with shrub *Acacia* and that it uses the abandoned burrows of other animals. Spiders and a wide range of other arthropods make up the majority of the food items in the diet although, by bulk, lizards *(Rhynchoedura ornata* and *Diplodactylus conspicillatus)* are one of the most important prey items. Further ecological details were provided by Pianka & Pianka (1976).

Nephrurus wheeleri **Loveridge, 1932 (Fig. 68)**

1909 *Nephrurus laevis* (part) Lucas & Le Souef. The Animals of Australia, Mammals, Reptiles and Amphibians: fig. p. 206.
1932 *Nephrurus wheeleri* Loveridge. Proc. New England Zool.Club 13: 31.

Type locality: Yandil, 30 miles NW of Wiluna, Western Australia.
Holotype: MCZ 32590.
1963 *Nephrurus wheeleri wheeleri* Storr. J.Roy.Soc.West.Aust. 46: 86; fig. 2 top left.
1963 *Nephrurus wheeleri cinctus* Storr. Ibid.: 86; fig. 2 middle left.
Type locality: Tambrey, Western Australia, (21°38'S, 117°37'E).
Holotype: WAM R4284.

D i a g n o s i s : Metatarsals I—IV one and a half or fewer times length of corresponding phalanges; phalangeal formulae 2-3-4-4-3 (manus), 2-3-4-4-4 (pes); dorsal pattern of head and nape without three dark bands; postmental scales enlarged anteriorly; dorsum covered by conical scales surrounded by conical rosette scales; six or fewer interorbital scales; vertical series of enlarged, tuberculate preocular scales; tail moderate. (**56, 61, 81**).

C o m m e n t s : Loveridge's (1932) description and diagnosis are thorough. *Nephrurus wheeleri* reaches a maximum SVL of 92 mm (Thomson & Hosmer 1963). This species, which resembles *N. asper*, is found only in the Murchison and Fortescue River districts of Western Australia (Fig. 59). *Nephrurus wheeleri* has been recorded from shrubland and open grassland in arid and semi-arid regions where it has a diet similar to that of its congeners (Pianka & Pianka 1976; Cogger et al. 1983).

Fig.68: Holotype of *Nephrurus wheeleri* Loveridge, 1932. MCZ 32950. SVL = 87 mm. (Scientific Photography Laboratory, U.C. Berkeley)

Phyllurus **Goldfuss, 1820**

1807 *Geckoides* Péron. Voyage de Découvertes aux Terres Australes, vol. 1: 450 (nomen oblitum).
Type species: "*Gecko platurus* Shaw" (= *Lacerta platura* White, 1790) by original designation.
1817 *Phyllurus* Oken. Isis von Oken, Jena 2(8): 1183 (nomen nudum).
1820 *Phyllurus* Goldfuss. Handbuch der Zoologie, vol. 3: 156.
Type species: *Phyllurus spinosus* Goldfuss, 1820 (pro vernacular of La Cépède, 1788, vol. 2: pl. 23, fig. 1) by monotypy.
1827 *Phyllura* Kaup. Isis von Oken, Jena 20: (nomen substitutum pro *Phyllurus* Oken, 1817).

S p e c i e s   r e f e r r e d : *Phyllurus caudiannulatus* Covacevich, 1975, *P. cornutus* (Ogilby, 1892), *P. platurus* (White, 1790), *P. salebrosus* Covacevich, 1975.

D i a g n o s i s : (Node 6) A monophyletic taxon diagnosed by the following characters: scleral ossicles fewer than 30; clavicular fenestrae tiny or absent; pectineal process of pubis enlarged; proximal joints of manus and pes kinked; tail depressed, leaf-shaped; limbs long and slender; head flattened, distinctly triangular; toes bear non-scansorial lamellae; skin of head co-ossified with skull; dorsum of body and tail bears spinose scales surrounded by rosettes. (15, 48*, 58*, **68**, 97*).

Within *Phyllurus* there are two diagnosable subgroups (Nodes 7 and 8) (see Fig. 17). Node 7, consisting of *P. caudiannulatus* and *P. platurus* is diagnosed by the following characters: Supraocular portion of frontal flattened; zero or one inscriptional ribs; anterior process of interclavicle terminates in a broadened disk; metacarpals V and IV shortest; no enlarged post-mental scales; rostral excluded from nostril; flank tubercles small. (5, 32-A, 37*, 45*, 81).

Node 8, including *Phyllurus cornutus* and *P. salebrosus*, is diagnosed by the following characters: Anterior process of interclavicle absent; epipubic cartilage greatly expanded; rosettes surrounding dorsal spines and tubercles also spinose; rostral contacts nostril; flank tubercles elongate, hooked. (38*, 47*, 83-B).

C o m m e n t s : *Phyllurus* was the first genus of carphodactylines to be discovered and described. The characteristic flattened leaf-shaped tail of the type species, *P. platurus* gave the name to the taxon. Péron (1807) used the name *Geckoides* but subsequent disuse has rendered this a nomen oblitum. The term "phyllure" was first used by Cuvier, but not as a binomial. Oken (1817) used the latinized *Phyllurus*, but as a nomen nudum. The first recognized acceptable usage of this generic name had long thought to be that of Schinz (1822), but Goldfuss (1820) used the combination *Phyllurus spinosus* and thus should be credited with authorship of the taxon. The absence of scansorial pads and the spiny skin of these geckos led a number of early workers to place members of this group in the Agamidae. Although Wagler (1830) clearly indicated their proper inclusion as gekkonids, Swainson (1839) wrote that the leaf-tailed lizard of New Holland served as a link to connect the geckos to *Stellio*.

The contents of the genus have been in flux since the description of the second species, *N. milii*, which has been variously assigned to the polyphyletic *Gymnodactylus* and to its own genus (along with *P. sphyrurus*), *Underwoodisaurus*. The results of this study do not concur with the views of Kluge (1967b) and Russell (1980) in their inclusion of these forms in *Phyllurus*. Rather, *milii* and *sphyrurus* should be considered members of the genus *Nephrurus* or perhaps members of a distinct genus, *Underwoodisaurus* (although this group is not diagnosable at present). The retention of these taxa in *Phyllurus* would leave this genus polyphyletic (see Fig. 17). Kluge (1967b) removed *P. vankampeni* from the genus, otherwise leaving Underwood's (1954) redefined *Phyllurus* intact. Kluge's (1967b) diagnosis of the genus is no longer adequate because some of the taxa he included have been removed. Covacevich (1975) provided good descriptions of all species but her key is not generally workable. The genus as a whole is distributed along the eastern coast of Australia from the northern Cape York Peninsula south to the area of Sydney. Members of the genus are by far the most well known Australian carphodactylines.

Key to the Species of *Phyllurus*

1a. Rostral contacts nostril 2
b. Rostral excluded from nostril 3
2a. Throat tuberculate . . . . *P. salebrosus*
b. Throat smooth . . . . *P. cornutus*
3a. Scales at metatarsal-phalangeal joint tuberculate (Fig. 69) . . . . *P. platurus*
b. Scales at metatarsal-phalangeal joint spinose . . . . *P. caudiannulatus*
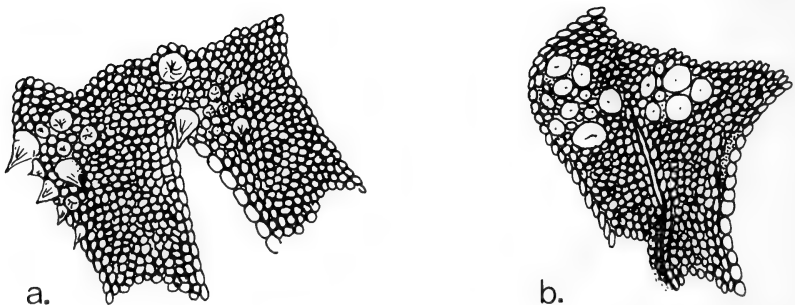

Fig.69: Metatarsal-phalangeal joint region of digits III and IV of (a) *Phyllurus caudiannulatus* and (b) *P. platurus*. Note the spinose tubercles in a (*Phyllurus* key character 3).
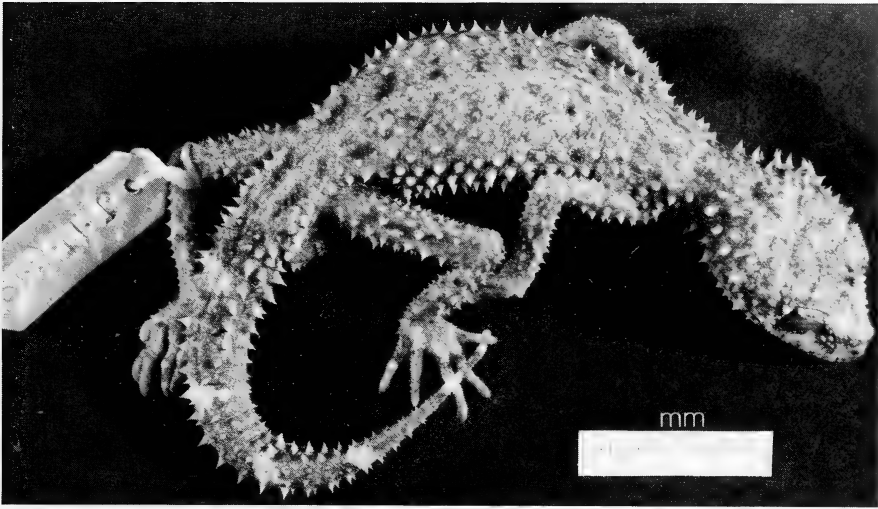
Fig.70: Holotype of *Phyllurus caudiannulatus* Covacevich, 1975. QM J15619. (Photo courtesy of Jeanette Covacevich, Queensland Museum)

Phyllurus caudiannulatus Covacevich, 1975 (Fig. 70)

1975 *Phyllurus caudiannulatus* Covacevich. Mem.Qld.Mus. 17: 297; figs. 2—4; pls. 36a, 37c, 38a, 39a, 40a.
Type locality: Bulburin State Forest, via Many Peaks, Queensland.
Holotype: QM J15619.

D i a g n o s i s : First autotomy plane in fifth caudal vertebra; flank tubercles small; preanal organs lacking; scales at metatarsal-phalangeal joint spinose; dorsal scales of body generally spinose; tail rounded or leaf-shaped; original tail bearing white bands.

C o m m e n t s : The description of *P. caudiannulatus* (Covacevich 1975) is detailed and useful. This small (maximum SVL 112 mm — AMNH 27326) species is known from Bulburin State Forest, to the south and west of Brisbane, and from Eungella National Park, all in south-eastern Queensland (Fig. 72). It has been collected under bark and on tree trunks and branches in cloud forest, primarily 350—950 m elevation. It has been reported from heights of 12 m in trees (Covacevich 1975). At Bulburin it is sympatric with *P. salebrosus*. Coleopterans have been recorded as natural dietary items (Rose 1974).

Phyllurus cornutus (Ogilby, 1892) (Fig. 71)

1892 *Gymnodactylus cornutus* Ogilby. Rec.Aust.Mus. 2: 8.
Type locality: Bellenden—Ker Ranges, NE Queensland. (A note with the specimen reads "Herbert River, Q. 13/10/91 Ogilby").
Holotype: AMS R749.

1897 *Phyllurus lichenosus* Günther. Novit.Zool. 4: 404; pl. XII.

Type locality: Mount Bartle Frere, Queensland.

Holotype: presumed lost.

1901 *Phyllurus cornutus* Garman. Bull.Mus.Comp.Zool. 39: 2.

1909 *Gymnodactylus cornutus* Lucas & Le Souef. The Animals of Australia, Mammals, Reptiles and Amphibians: 209.

1950 *Gymnodactylus spyrurus* Barrett. Reptiles of Australia: 31 (non *Gymnodactylus sphyrurus* Ogilby, 1892; lapsus pro *Gymnodactylus cornutus* Ogilby, 1892).

1954 *Phyllurus cornutus* Underwood. Proc.Zool.Soc. London 124: 474.

1976 *Phyllurus cornutum* Swanson. Lizards of Australia: 18; pl. 29.

1979 *Phyllurus cornutus* Cogger. Reptiles and Amphibians of Australia, revised (2nd) ed.: 174; figs. 78, 423, 424.

D i a g n o s i s : Rostral contacts nostril, preanal pores absent, throat smooth, flank tubercles enlarged and hooked; attenuated tail tip > 1/3 total tail length.

C o m m e n t s : Ogilby's (1892) description is adequate, although a variable feature — a spinate knob on the brillar flap — is stressed as the diagnostic character. Günther (1897) described *P. lichenosus* based on his specimen's variance from *P. cornutus* in this character. This is one of the largest Australian geckos, reaching 144 mm SVL (AMS

Fig.71: Holotype of *Gymnodactylus cornutus* Ogilby, 1892 (= *Phyllurus cornutus*). AMS R749. (Photo courtesy of The Australian Museum)

42163). Populations in the southern parts of the range tend to be of smaller size than those from the Cape York Peninsula. There are three disjunct populations of *Phyllurus cornutus*, all to the east of the Great Dividing Range, located in the northern Cape York near Coen, in the area between Townsville and Cooktown, and in a strip from extreme south-eastern Queensland through central coastal New South Wales (Fig. 72). Most known localities are above 300 m elevation. A population near Stanthorpe (Qld.) is recognized as distinct (Covacevich 1975) and may warrant specific recognition (J. Covacevich pers. comm.). Covacevich (1975) stated that similarly disjunct patterns are
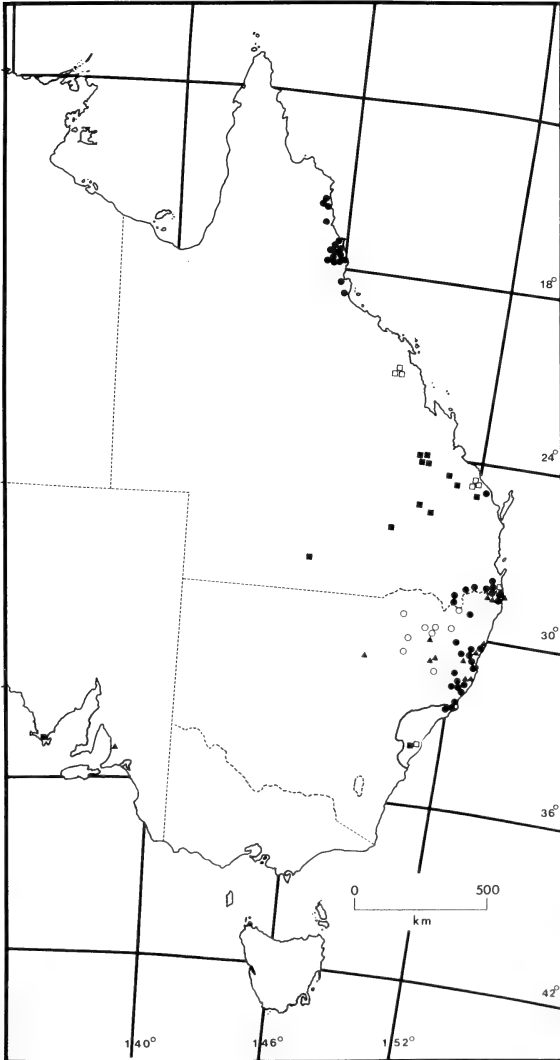
Fig.72: Distribution of *Phyllurus cornutus* (closed circles), *P. caudiannulatus* (open squares), *P. salebrosus* (closed squares), *Nephrurus sphyrurus* (open circles) and *Phyllurus platurus* (area bounded by dark line in the region of Sydney, N.S.W.). Closed triangles represent records of *P. platurus* probably referable to *P. caudiannulatus*.

seen in the distribution of *Tropidechis carinatus, Leiolopisma challengeri, Lechriodus fletcheri* and *Litoria chloris*.

This species occurs in virgin and disturbed areas of cloud forest and adjacent sclerophyll forests, usually found on trees, to a height of 10 m (Loveridge 1934). At Stanthorpe it is found in a granite boulder area with relatively open vegetation (Covacevich 1975). Bustard (1965) recorded this species from cave mouths and the trunks of *Laportea gigas* in northern New South Wales. Bustard (1965) and Rösler (1981) discussed behavior and feeding in captivity. *Phyllurus cornutus* is chiefly an arthropod feeder in the wild. The species is a known prey item in the diet of the elapid *Demansia psammophis* (see Shine 1980).

Phyllurus platurus (White, 1790) (Figs. 73,74)

1790 *Lacerta platura* White. Journal of a Voyage to New South Wales: 246; pl. 32 (fig. 2).
Type locality: New South Wales.
Holotype: probably BMNH xxii.98.a (cleared and stained specimen) (fide Covacevich 1975).
1797 *Stellio phyllurus* Schneider. Amphibiorum Physiologiae Specimen Secundeum. 2nd ed.: 31 (nomen substitutum pro *Lacerta platura* White, 1790).
1802 *Stellio platurus* Daudin. Histoire Naturelle Générale et Particulière des Reptiles, vol. 4: 24.
1802 *Lacerta platura* Shaw. General Zoology, vol III, pt. I: 247.
1804 *Agama grandoculis* La Cépède. Ann.Mus.Natl.Hist.Nat. Paris 4: 191.
Type locality: Nouvelle-Hollande.
Holotype: MNHN (specimen number unknown).
1804 *Lacerta platura* Hammer. Observationes Zoologicae: 266.
1807 *Geckoides platurus* Péron. Voyage de Découvertes aux Terres Australes, vol. 1: 450.
1820 *Phyllurus spinosus* Goldfuss. Handbuch der Zoologie, vol. 3: 156 (nomen substitutum pro *Lacerta platura* White, 1790; pro vernacular of La Cépède 1788, vol. 2: pl. 23, fig. 1).
1820 *Agama platyura* Merrem. Versuch eines Systems der Amphibien: 51 (nomen substitutum pro *Lacerta platura* White, 1790).
1820 *Agama discosura* Merrem. Ibid.: 51 (pro vernacular "lézard discosure" of La Cépède 1804).
Type locality: Nova Hollandia.
Holotype: MNHN (specimen not located).
1822 *Phyll(urus) novaehollandiae* Schinz. Das Thierreich eingetheilt nach dem Bau der Thiere von Cuvier: 79 (ex Cuvier manuscript; nomen substitutum pro *Lacerta platura* White, 1790).
1825 *Phyllurus cuvieri* Bory de Saint-Vincent. Dictionnaire Classique d'Histoire Naturelle, vol.7: 183.
Type locality: environs de Port Jackson, New South Wales.
Holotype: MNHN (presumed lost).

1825 *P(hyllurus) whitii* Gray. Ann.Phil. (2)10: 198.

Type locality: not given.

Holotype: BMNH, specimen not located.

1826 *Phyllurus platurus* Fitzinger. Neue Classification der Reptilien nach ihren natürlichen Verwandschaften: 47.

1827 *Phyllura discosura* Kaup. Isis von Oken, Jena 20: 613 (nomen substitutum pro *Phyllurus* Oken, 1817).

1827 *Phyllura grandoculis* Kaup. Ibid.: 613 (nomen substitutum pro *Phyllurus* Oken, 1817).

1830 *Gymnodactylus platyurus* Wagler. Natürliches System der Amphibien: 144.

1831 *Cyrtodactylus platura* Gray. In: The Animal Kingdom Arranged in Conformity with its Organization by the Baron Cuvier, vol. 9: 52.

1833 *Gecko platycaudus* Schinz. Naturgeschichte und Abbildungen der Reptilien: 75; pl.17 (fig. 3) (nomen substitutum pro *Stellio phyllurus* Schneider, 1797).

1834 *Gymnodactylus (Phyllurus) phyllurus* Wiegmann. Herpetologia Mexicana: 19.

1836 *Gymnodactylus phyllurus* Duméril & Bibron. Erpétologie Générale, vol. 3: 428.

1839 *Phyllurus australis* Swainson. The Natural History of Fishes, Amphibians, and Reptiles, vol.2: 370 (fig. 123a) (nomen substitutum pro *Phyllurus platurus* (White, 1790)).

1842 *Phyllurus cuvierii* Bory de Saint-Vincent. Traité Elementaire d'Erpétologie ou l'Histoire Naturelle des Reptiles: 130 (lapsus pro *Phyllurus cuvieri* Bory de Saint-Vincent, 1825).

1843 *Gymnodactylus (Phyllurus) platurus* Fitzinger. Systema Reptilium: 92.

1845 *Phyllurus platurus* Gray. Catalogue of the Specimens of Lizards in the Collection of the British Museum: 176.

1845 *Phyllurus inermis* Gray. Ibid.: 176.

Type locality: Australia.

Holotype: BMNH xxii.100.a.

1885 *Gymnodactylus platurus* Boulenger. Catalogue of Lizards in the British Museum, vol. 1: 49.

1909 *Gymnodactylus phyllurus* Lucas & LeSouef. The Animals of Australia, Mammals, Reptiles, and Amphibians: 209.

1910 *G(ymnodactylus) platyurus* Werner. Die Fauna Südwest- Australiens, II: 453.

1934 *Phyllurus platurus* Loveridge. Bull.Mus.Comp.Zool. 77: 298.

1950 *Gymnodactylus platurus* Barrett. Reptiles of Australia: 31.

1954 *Phyllurus platurus* Underwood. Proc.Zool.Soc. London 124: 474.

D i a g n o s i s : Rostral excluded from nostril; scales at metatarsal-phalangeal joint flat, tuberculate; preanal organs absent; flank tubercles small; original tail without bands; first autotomy plane in sixth caudal vertebra.

C o m m e n t s : *Phyllurus platurus* was the first species of carphodactyline gecko to be described. Its distinct morphology, coupled with its abundance in and around Sydney, Australia's oldest and largest population center, has been responsible for the many references relating to this animal. White's (1790) description is short but, with the ac-

Fig.73: Presumed holotype of *Lacerta platura* White, 1790 (= *Phyllurus platurus*). BMNH xxii.98.a. (Photo courtesy British Museum (Natural History))

companying illustration, is sufficient to diagnose the species from other congeners except *P. caudiannulatus*. Numerous names have been substituted for *platurus*. This was especially true during the first half of the nineteenth century. Gray's (1845) *P. inermis* is based on a *P. platurus* with a typical smooth-scaled regenerated tail.

Girard (1857: 303) wrote "this species, owing to its uncommon aspect, has often attracted the attention of naturalists and iconographists, so that we may say that it is pretty generally well known". Unfortunately this is not true. As for most carphodactylines, little is known of the biology of this species. Swanson (1976) reports a maximum total length of 150 mm. The largest individual museum specimen measures 95.9 mm SVL (Covacevich 1975). The southern leaf-tailed gecko is distributed in a small area of coastal south-central New South Wales (Fig. 72). This range corresponds to the Sydney-Hawkesbury Sandstone (Breeden & Breeden 1972). It is likely that specimens reported from Queensland localities are either *P. cornutus*, or more likely *P. caudiannulatus*. It occurs in forests, in association with rocks (Cogger et al. 1983), in small wind-blown caves and in houses and garages (Cogger 1967). It is chiefly saxicolous and spends the daylight hours partially active in deep rock crevices. Bory de Saint-Vincent (1825) gave the earliest information on carphodactyline biology and stated that *P. cuvieri* (= *P. platurus)* feeds on insects and aquatic larvae in the rocky areas around Port Jackson (= Sydney). The reference to aquatic larvae is doubtful but the species is chiefly insec-
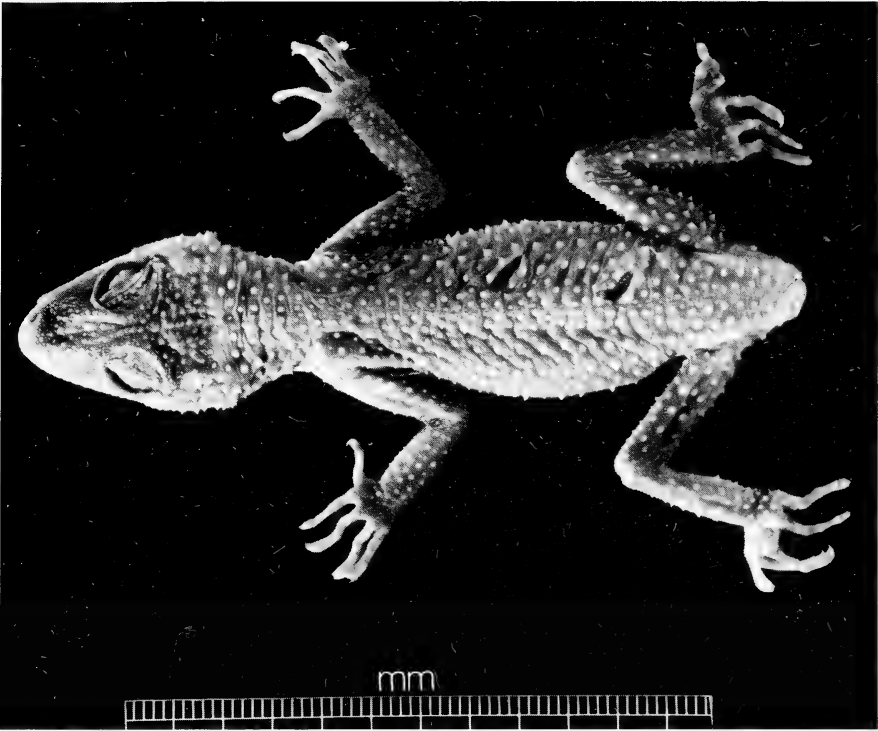
Fig.74: Holotype of *Phyllurus inermis* Gray, 1845 (= *Phyllurus platurus*). BMNH xxii.100.a. (Photo courtesy British Museum (Natural History))

tivorous. Green (1973) reported spiders *(Hemidoea)*, coleopterans, lepidopterans and acridids in the diet. Eggs are laid in rock crevices and deposition sites may be communal and up to 16 individuals have been found in a single rock crevice (Green 1973). Embryos are at stage 29 of development at the time of ovoposition (Shine 1983b). Covacevich (1975) gave information on tail break frequencies in this species as well as bivariate plots of several body size parameters for this and other *Phyllurus*. Mebs (1973) and Green (1973) described the defensive response of this species. Red mite infestations are common and cats, rodents, owls, bats and *Antichinus stuartii* (a marsupial mouse) are probable predators (Green 1973).

Phyllurus salebrosus Covacevich, 1975 (Fig. 75)

1975 *Phyllurus salebrosus* Covacevich. Mem.Qld.Mus. 17: 300; figs. 3—4; pls. 36c, 37a, 38b, 39b, 40b.
Type locality: Monto, SE Queensland.
Holotype: QM J8142.
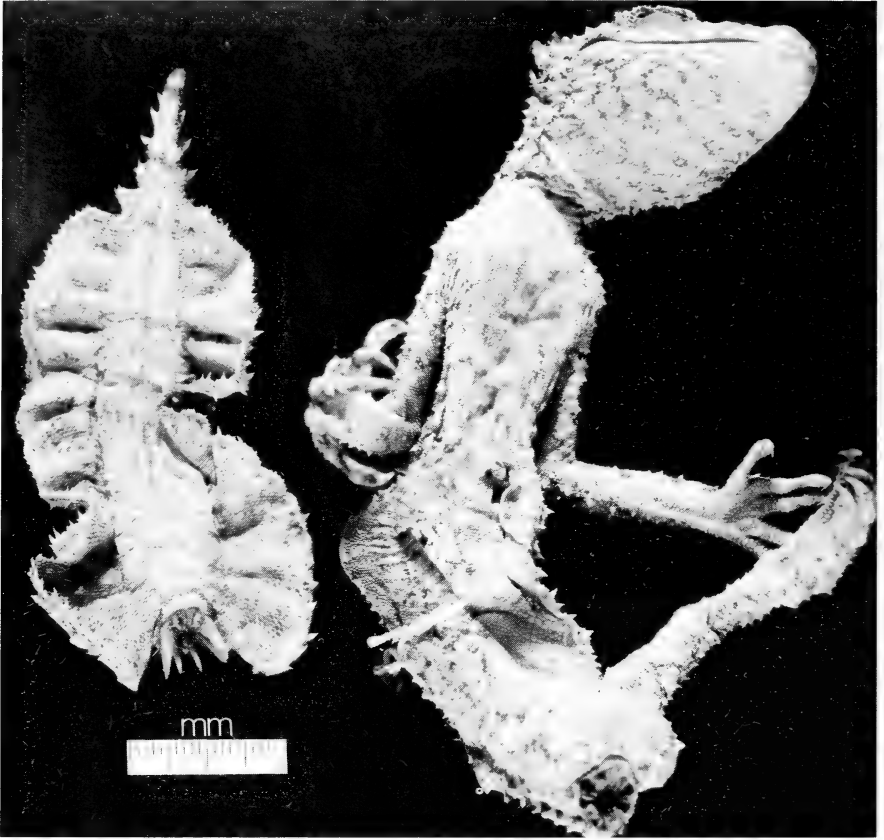
Fig.75: Holotype of *Phyllurus salebrosus* Covacevich, 1975. QM J8142. (Photo courtesy of Jeanette Covacevich, Queensland Museum)

D i a g n o s i s : Rostral contacts nostril; throat tuberculate; flanks with enlarged tubercles; preanal pores present; attenuated tail tip $<$ 1/3 total tail length. **(92)**.

C o m m e n t s : *Phyllurus salebrosus* is among the largest Australian carphodactylines at 143 mm SVL (QM J33732). It is rare throughout its range which extends over parts of coastal and mid southern Queensland (Fig. 72). Records of specimens from Sydney (N.S.W.) and Port Lincoln (S.A.) are surely in error. It has been collected from areas of granite rocks, sandstone and on a cave roof (Covacevich 1975). It may be arboreal, saxicolous or cavernicolous in different areas and generally occurs in more open habitats than its morphologically similar, but allopatric congener *P. cornutus*. It is primarily insectivorous.

Rhacodactylus Fitzinger, 1843

(Note: Members of the subgenus *Pseudothecadactylus* follow other *Rhacodactylus* spp.)

1843 *Rhacodactylus* Fitzinger. Systema Reptilium: 90.
Type species: *A(scalabotes) leachianus* Cuvier, 1829 by original designation.
1866 *Correlophus* Guichenot. Mém.Soc.Hist.Nat. Cherbourg 12: 249.
Type species: *Correlophus ciliatus* Guichenot, 1866 by monotypy.
1873 *Ceratolophus* Bocage. J.Sci.Mat.Phys.Nat. Lisboa 4: 204 (non *Ceratolophus* Kieffer, 1899 = Diptera).
Type species: *Ceratolophus hexaceros* Bocage, 1873 by monotypy.
1878 *Chameleonurus* Boulenger. Bull.Soc.Zool. France 3: 68.
Type species: *Chameleonurus trachycephalus* Boulenger, 1878 by monotypy.
1889 *Chamaeleonurus* Carus. Zool.Anz., Leipzig: 83 (ex errore pro *Chameleonurus* Boulenger, 1878).
1972 *Ceratophus* Mufti & Hafiz. Biologia (Lahore) 18: 191 (lapsus pro *Ceratolophus* Bocage, 1873).

S p e c i e s   r e f e r r e d : *Rhacodactylus auriculatus* (Bavay, 1869); *R. chahoua* (Bavay, 1869); *R. ciliatus* (Guichenot, 1866); *R. leachianus* (Cuvier, 1829); *R. sarasinorum* Roux, 1913; *R. trachyrhynchus* Bocage, 1873; *R. (Pseudothecadactylus) australis* (Günther, 1877); *R.(P.) cavaticus* Cogger, 1975; *R.(P.) lindneri* Cogger, 1975.

D i a g n o s i s : *Rhacodactylus*, as previously construed was a metataxon, a paraphyletic grouping which excludes some members of the natural group united by a suite of characters at Node 18. Thus, the traditional New Caledonian group of *Rhacodactylus* consists of the taxa sharing the character states present at Node 18 but lacking those at Node 20. The following characters diagnose the species of *Rhacodactylus* including those of the subgenus *Pseudothecadactylus*: Supraocular portion of frontal deeply furrowed or concave; fronto-parietal suture straight; overlap of jugal and infraorbital process of prefrontal extensive; metatarsals III and IV parallel; lateral pair of cloacal bones absent; juvenile color pattern with paravertebral rows of light-colored spots; aural opening partially occluded by skin folds; digital scansors broadly dilated; apical pads single, medial; tail with subcaudal lamellae. (5, **9**, 13, **59**, 62, 70, 7ᐟ

Within *Rhacodactylus* (sensu stricto) a single resolvable subgrouping occurs (apart from those characters diagnosing *Pseudothecadactylus*). Represented by Node 19 oι. the cladogram this unites *R. chahoua* and *R. ciliatus*. This clade is diagnosed by the following characters: anteriormost autotomy septum in fifth caudal vertebra; webbing between digits IV and V present; folds of loose skin on face of hindlimbs. (30, 89, 90).

C o m m e n t s : (comments for *Pseudothecadactylus* follow subgeneric synonymy): The genus *Rhacodactylus* includes some of the largest geckos in the world (Bauer & Russell 1986; Russell & Bauer 1986). Because of this size there have been a great many references to the taxon (see Bauer 1985b), although few have made substantial additions to the knowledge of *Rhacodactylus*. Cuvier described *R. leachianus* in 1829 as a member of the genus *Ascalobotes*. This generic designation was uniformly miscited as *Platydactylus*. The species remained in this genus until Fitzinger (1843) erected the

subgenus *Rhacodactylus* within *Hoplodactylus*. The outlandish morphologies of
several of the species resulted in the erection of new genera based solely on these
autapomorphic charaters. Nomenclature stabilized after the review of New Caledonian
geckos by Boulenger (1883). *Rhacodactylus* occurs over much of New Caledonia,
although no reliable records exist from the west coastal plains areas. Records from the
Loyalty Islands are all anecdotal. Records from the Isle of Pines and the Belep Isles may
be valid, although Roux (1913) considered the genus as being restricted to New
Caledonia proper. All species are primarily arboreal and as many as four species may
occur in sympatry. Remarks on the biology and systematics of the species may be found
in Boulenger (1883), Roux (1913), Mertens (1964a) and Meier (1979). Jouan (1863) and
Bavay (1869) report that the indigenous people of New Caledonia, the Kanaks, have a
variety of superstitions regarding members of the genus. This is still true to some extent
and most people will avoid these animals, which are known by the vernacular
"cameleons".

Key to the Species of *Rhacodactylus*

1a. All digits clawed 2
b. Digit I of manus clawless .... subgenus *Pseudothecadactylus*
2a. Body with loose folds of skin along throat and flanks, digits half-webbed ... 3
b. Body without lateral folds, digits less than one third webbed 4
3a. Rostral contacts nostril .... *R. chahoua*
b. Rostral excluded from nostril .... *R. leachianus*
4a. Pair of posteriorly converging ciliated crests on dorsum .... *R. ciliatus*
b. Dorsal scales generally homogeneous 5
5a. Head with raised bosses or rugosities 6
b. Head smooth, no bosses or rugosities .... *R. sarasinorum*
6a. Snout rugose .... *R. trachyrhynchus*
b. Raised orbital and aural bosses present, snout smooth .... *R. auriculatus*

Rhacodactylus auriculatus (Bavay, 1869) (Fig. 76)

1869 *Platydactylus auriculatus* Bavay. Mém.Soc.Linn. Normandie 15: 6.
Type locality: Mont d'Or (= Mont Dore), Nouvelle-Calédonie.
Holotype: EMNB (presumed lost).
1873 *Ceratolophus hexaceros* Bocage. J.Sci.Mat.Phys.Nat. Lisboa 4: 205.
Type locality: Nouvelle Calédonie.
Syntypes: MLI (specimen number unknown, destroyed by fire).
1878 *Platydactylus (Ceratolophus) auriculatus* Sauvage. Bull.Soc.Philomat., Paris (7)3:
67.
1881 *Ceratolophus auriculatus* Bocage. J.Sci.Mat.Phys.Nat. Lisboa 8: 130.
1883 *Rhacodactylus auriculatus* Boulenger. Proc.Zool.Soc. London 1883: 127.
1920 *Ceratolophus auriculatus* Woodland. Q.J.Microscop.Sci. 65: 63.
1932 *Rhacodactylus auriculatus* Burt & Burt. Bull.Amer.Mus.Nat.Hist. 63: 479.
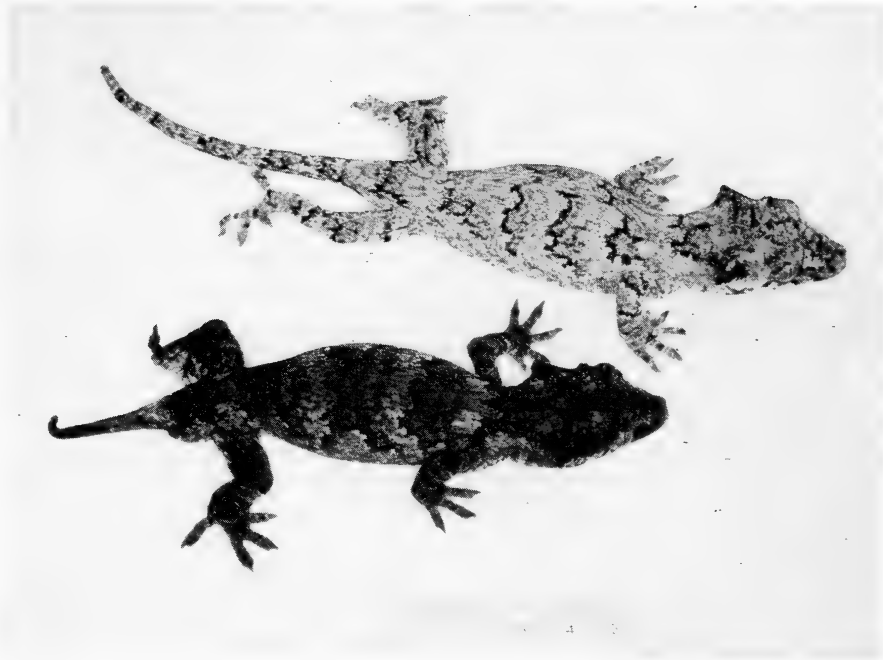
Fig.76: Two color phases of *Rhacodactylus auriculatus* (Bavay, 1869) from Touaourou, New Caledonia. (Scientific Photography Laboratory, U.C. Berkeley)

1949 *Gecko ceratolophus* Boring et al. Peking Nat.Hist.Bull. 17: 85 (lapsus pro *Ceratolophus auriculatus* (Bavay, 1869) ad Woodland (1920)).
1964 *Rhacodactylus auriculatus* Mertens. Zool.Garten, Leipzig, N.F. 29: 52.
1972 *Ceratophus auriculatus* Mufti & Hafiz. Biologia (Lahore) 18: 191 (lapsus pro *Ceratolophus auriculatus* (Bavay, 1869) ad Woodland (1920)).
1979 *Rhacodactylus auriculatus* Meier. Salamandra 15: 113.

D i a g n o s i s : This species is diagnosed by the following characters: lateral prong of postfrontal distinctly ventrally curved; parietal crest present; lateral lip of quadrate extended in a flange; fewer than 30 scleral ossicles; two to four inscriptional ribs; juvenile color pattern as adult; aural opening free of skin folds; first infralabials may contact behind mental; folds of loose skin on posterior face of hindlimb present; preanal organs extend onto thighs; pygal region tapers into post-pygal region. (6, 10, 12, 15, 32B, **62**, **70**, 80, 90, 93, **102**).

C o m m e n t s : The large knobs on the skull of this species make it difficult to confuse with any other. It is unclear how Bocage (1873) could have failed to recognized his *Ceratolophus hexaceros* from Bavay's (1869) superb description of *Platydactylus auriculatus*. This is the most well known of the members of the genus and over 100 specimens exist in museum collections.

Rhacodactylus auriculatus is one of the smallest members of the genus with a max-
imum SVL of 125 mm (Boulenger 1883; MNHN 1974-805). It is distributed over much
of southern and south-central New Caledonia (Fig. 77), chiefly in association with
ultramafic soils and their associated vegetation (Figs. 30,84). Concentrations within the
range of the species probably reflect ease of access and collection concentration in these
areas. It has been collected from a variety of shrubs and smaller trees (Bavay 1869;
Meier 1979; Böhme & Henkel 1985; pers. obs.).

While Bavay (1869) found the species in montaine forest I have collected it at sea level
all along the south-east coast of New Caledonia and it seems likely that lower elevation,
drier forests are more typical habitats for this gecko. One individual was collected on
a tree trunk 3 m from high tide. Individuals may also spend substantial periods of time
on the ground as they are frequently seen crossing dirt roads between forest stands
south of Yaté. This species is occasionally encountered basking on tree trunks 1—3 m
above the ground during daylight hours (Meier 1979; pers. obs.). Sameit (1985) and
Böhme & Henkel (1985) included additional information about the habitat of *R.
auriculatus*. Reported dietary items include flowers of the *Geiossois*, snails (Bavay
1869), crickets and *Bavayia sauvagii* (Bauer & DeVaney 1987). It is probable that spiders
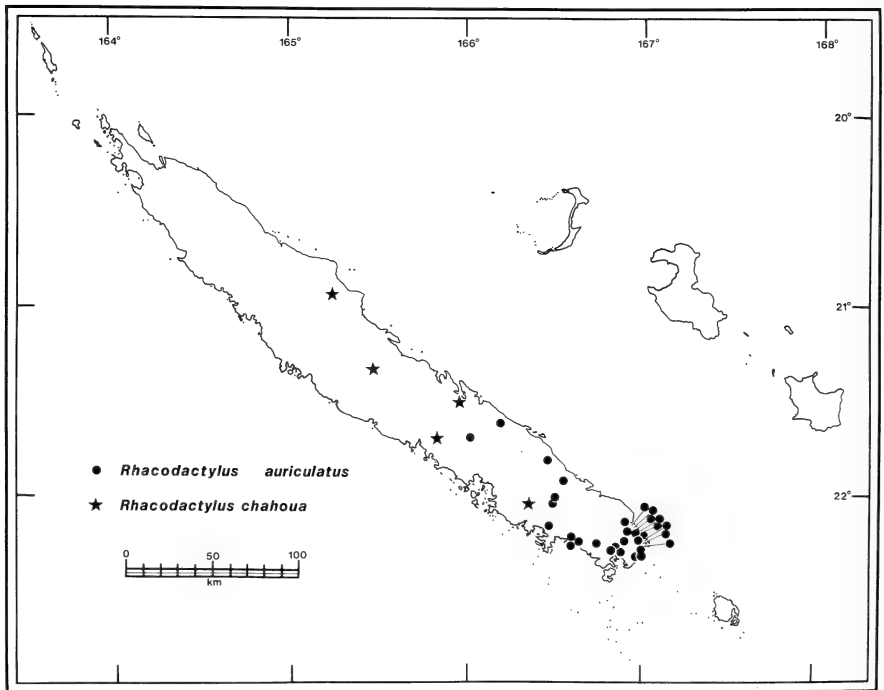
Fig.77: Distribution of *Rhacodactylus auriculatus* (circles) and *R. chahoua* (stars) in New
Caledonia.

and a wide variety of other arthropods are also important in the diet of this species. Mertens (1964a) reported on the frugivorous habits of this species in captivity. *Rhacodactylus auriculatus* is highly variable in color and a wide range of pattern phases may be found at one locality (Böhme & Henkel 1985). The species is oviparous and lays two eggs (approximately 25 x 11 mm). Repeated copulations are common in captivity (K. McCloud pers. comm.). No laying sites have been found in New Caledonia and it is possible that the species can breed all year. Incubation period ranges from 42—48 days (Henkel 1986a) to about 60 days (K. McCloud pers. comm.). Mites are frequently present in mite-pockets on the hindlimbs (Böhme & Henkel 1985; pers. obs.).

Fig.78: Neotype of *Rhacodactylus chahoua* (Bavay, 1869). CAS 156692 (SVL = 136 mm).

Rhacodactylus chahoua **(Bavay, 1869) (Fig. 78)**

1869 *Platydactylus chahoua* Bavay. Mém.Soc.Linn. Normandie 15: 3.

Type locality: Vallée d'Amoa, near St. Thérèse, approx. 15 km NW of Poindimié, New Caledonia. (Type locality of Bavay (1869) = Kanala, Lifou (sic!, probably Canala, New Caledonia)).

Holotype: EMNB (presumed lost).

Neotype: CAS 156692 (designated by Bauer 1985a).

1878 *Platydactylus (Rhacodactylus) chahoua* (part) Sauvage. Bull.Soc.Philomat., Paris (7)3: 66.

1879 *Chameleonurus chahoua* (part) Boulenger. Bull.Soc.Zool. France 4: 142.

1883 *Rhacodactylus chahoua* Boulenger. Proc.Zool.Soc. London 1883: 125; pl. XXI (figs. 1,1a—1d).

D i a g n o s i s : This species is diagnosed from its congeners by the characters at Node 19 and from *R. ciliatus* by the presence of mandibular folds of skin, absence of ciliated dorsal crests, non-expanded lateral quadrate conch flange, small superciliary scales and homogeneous dorsal scalation. (91).

C o m m e n t s : Bavay (1869) provided a detailed diagnosis and description for this species. The specific epithet, *chahoua*, is supposed to be derived from a Kanak word for the devil, with which the giant forest geckos were associated by the natives (Bavay 1869). Bauer (1985a) provides a brief summary of the taxonomic confusion surrounding this animal and its congener *R. trachyrhynchus*. This species, as well as several other carphodactylines named by Bavay, has been the source of numerous taxonomic debates. The types of Bavay were deposited in the Musée de l'Ecole de Médecine Navale in Brest (Roux 1913) but are now presumed lost. Bauer (1985a) designated a neotype in an effort to permanently stabilize the name.

This species, which grows to a maximum SVL of 147 mm (CAS 156691) is known from five localities in south and central New Caledonia. Bavay's (1869) type locality (Kanala, Lifou) is assumed to be an error for Canala, New Caledonia. All localities are on or very near large rivers and are associated with primary forest patches with relatively high rainfall. Bauer (1985a) discussed ontogenetic and sexual variation in *R. chahoua* as well as feeding and courtship behavior in captivity. Incubation (approximately 85 days) is described by Henkel (1981, 1986a) along with other aspects of husbandry. A large number of this species have now been bred and raised in captivity (pers. comm. H. Meier, F.W. Henkel). It is probable that this species is associated with larger trees (Bauer 1985a; Sameit 1985; Henkel 1986b) and that it only rarely descends trunks below the level of the lowest branches.

Rhacodactylus ciliatus **(Guichenot, 1866) (Fig. 79)**

1866 *Correlophus ciliatus* Guichenot. Mém.Soc.Hist.Nat. Cherbourg 12: 249; pl. VIII.

Type locality: Nouvelle-Calédonie.

Lectotype: MNHN 701a, here designated.

Paralectotype: MNHN 701

1883 *Rhacodactylus ciliatus* Boulenger. Proc.Zool.Soc., London 1883: 128.

Fig.79: Lectotype of *Correlophus ciliatus* Guichenot, 1866 (= *Rhacodactylus ciliatus*). MNHN 701a. (Photo courtesy of Muséum National d'Histoire Naturelle, Paris)

1934 *Correlophus ciliatus* Brongersma. Zool.Meded. 17: 165.
1964 *Rhacodactylus ciliatus* Mertens. Zool.Garten, Leipzig, N.F. 29: 52.

D i a g n o s i s : This species is diagnosed from its congeners by the characters at node 19 and from *R. chahoua* by the presence of a parietal crest; expanded lateral lip of the quadrate; dorsal body scalation heterogeneous, with paired ciliated crests from temporal region converging at shoulders; nostril excluded from rostral; enlarged supracilliary scales; original tail tip oar-shaped. (10, 12, **78, 79**).

C o m m e n t s : *Rhacodactylus ciliatus* is the least well known of the New Caledonian geckos because all of the numerous specimens were collected in the nineteenth century and few have associated data. Guichenot (1866) created the genus *Correlophus* for the species. His description is adequate and is accompanied by an engraving. Bavay (1869) believed that it should be relegated to a subgenus of *Platydactylus* but did not make the taxonomic shift himself.

The only known localities are Ciu and Noumea (Fig. 86), although it is probable that the later is in reality the place of shipment of the specimen rather than of collection. Bavay (1869) stated that this species lived in montaine forests and that it was only to be seen during rains. *Rhacodactylus ciliatus* attains a maximum SVL of 106 mm (NHW 17927-1) and is probably similar to its closest relative, *R. chahoua*, in its biology. Mites are common on this species. This is the only member of the genus for which reproductive mode is unknown.

Rhacodactylus leachianus (Cuvier, 1829) (Fig. 80)

1829 *A(scalabotes) leachianus* Cuvier. Le Règne Animal, vol.2: 54.
Type locality: not given.
Holotype : MNHN 6687
1831 *Pteroplura (Gecko) leachianus* Gray. The Animal Kingdom Arranged in Conformity with its Organization by the Baron Cuvier, vol. 9: 49.
1833 *Gecko leachii* Schinz. Naturgeschichte und Abbildungen der Reptilien: 73 (nomen emendatum pro *Gecko leachianus* (Cuvier, 1829)).
1836 *Platydactylus leachianus* Duméril & Bibron. Erpétologie Générale, vol.3: 315.
1843 *Hoplodactylus (Rhacodactylus) leachianus* Fitzinger. Systema Reptilia: 90.
1869 *Platydactylus leachianus* Bavay. Mém.Soc.Linn. Normandie 15: 3.
1873 *Rhacodactylus leachianus* Bocage. J.Sci.Mat.Phys.Nat. Lisboa 4: 201.
1873 *Rhacodactylus aubrianus* Bocage. Ibid.: 202.
Type locality: Nouvelle Calédonie.
Syntypes: MLI (specimen number unknown, destroyed by fire).
1881 *Rhacodactylus aubryanus* Bocage. J.Sci.Mat.Phys.Nat. Lisboa 8: 127 (ex errore pro *Rhacodactylus aubrianus* Bocage, 1873).
1913 *Rhacodactylus leachianus aubryanus* Roux. Nova Caledonia, Zoologie I(II): 96.
1932 *Rhacodactylus leachianus* Burt & Burt. Bull.Amer.Mus.Nat.Hist. 63: 479.

D i a g n o s i s : This species is diagnosed by the following characters: Skin of head co-ossified with skull; lateral prong of postfrontal distinctly downcurved; scleral ossicles fewer than thirty in number; two to four inscriptional ribs present; three to four abdominal ribs present; fewer than thirty caudal vertebrae; rostral scales excluded from nostril; webbing between digits IV and V present; folds of loose skin on posterior face of hindlimb; folds of skin at mandibular margins; ventral tail sulcus present. (1, 6, 15, 25, 32B, **33**, **79**, 89, 90, 91, 104).

C o m m e n t s : This is the largest extant species of gecko (Bauer & Russell 1986; Russell & Bauer 1986) reaching a maximum SVL of 245 mm (CAS 165890). Cuvier's (1829) description is woefully inadequate. It follows in its entirety: "Nous en avons une espèce lisse, à pieds palmés (*A. leachianus* Nob.)". Duméril & Bibron (1836) provided an adequate description of the species and illustrated the digits. *Rhacodactylus aubrianus* Bocage, 1873 would appear to be merely a particular ontogenetic phase or aberrant form. Unfortunately, the only known specimens bearing this name, along with other rare New Caledonian carphodactylines, were destroyed by fire in the Lisbon Museum. There is a wide range of variability, particularly in coloration, within this

Fig.80: Holotype of *A(scalabotes) leachianus* Cuvier, 1829 (= *Rhacodactylus leachianus*). MNHN 6687. (Photo courtesy of Muséum National d'Histoire Naturelle, Paris)

species. Typically, juveniles have distinct whitish spots, sub-adults have large pinkish lateral bands and adults assume a more uniform drab dorsal pattern. However, some animals remain more or less reticulate throughout life. Although the possibility that two species are present is unlikely, there may be some populational variation.

The provenance of *R. leachianus* was unknown until 1869, when Bavay confirmed its presence in New Caledonia. The species is distributed over most of the east coast of

Fig.81: Primary rainforest on the slopes of the Massif de Panié, northeast coastal New Caledonia — habitat of *Rhacodactylus leachianus*.

the island as well as in mountainous areas in the southern half of the island (Figs. 81,82). Most localities appear to be associated with rivers and humid forest vegetation from sea-level to 1100 m (Mertens 1964a), although individuals have been collected in slightly drier regions in the far south in association with ultramafic soils and edaphic vegetation (Fig. 82). Boulenger (1885a) recorded a specimen from the Isle of Pines off the southern tip of New Caledonia. This may be a legitimate record, given the similarity in paleogeography and geological structure of the Isle of Pines to the mainland of New Caledonia. Jouan (1864) reported that there was a giant gecko called "paït" by the natives at Hienghène (a known *R. leachianus* locality) and "tint" by those at Belep, the island group to the north of New Caledonia. It too shares certain features with the mainland, which would suggest that this record may have some validity, although no specimens exist from this area.

Bocage (1881) stated that *R. leachianus* was common in New Caledonia, my observations would tend to support that statement today, although habitat alteration threatens this and other forest geckos in New Caledonia (Meier 1979; Bauer 1985a; Bauer in press). Jouan (1863) described a 400 mm gecko from Hienghène which is found under bark and in the forks of rotten trees. Bavay (1869) also reported this species from boulder areas and permanently dispelled the belief that webbed feet in gekkonids were associated with aquatic habits. I have frequently seen this species climbing on the
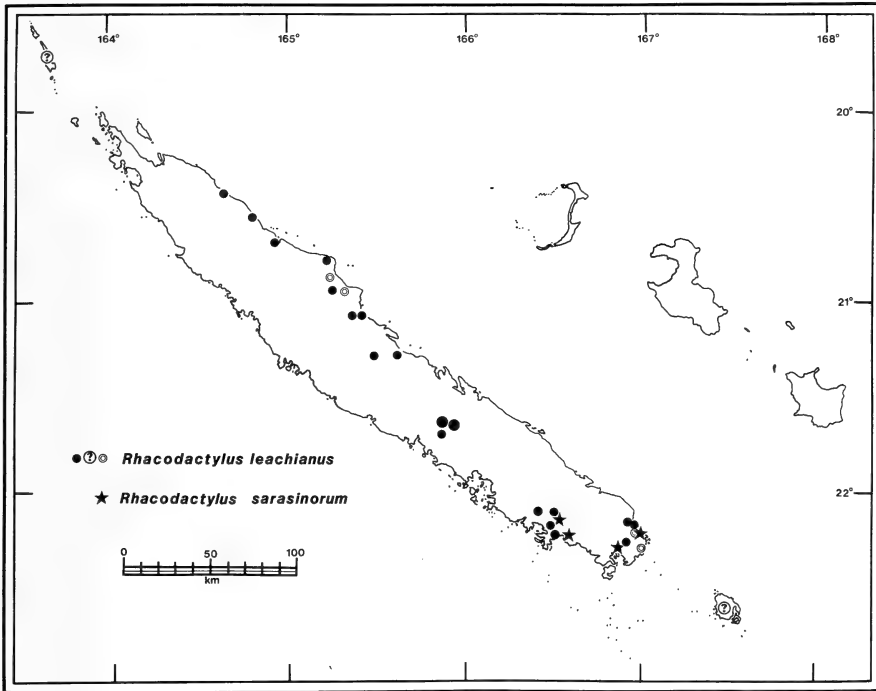
Fig.82: Distribution of *Rhacodactylus leachianus* (circles) and *R. sarasinorum* (stars) in New Caledonia. Question marks indicate doubtful island localities of *R. leachianus*. Circles within circles represent sight records of *R. leachianus*.

trunks of large trees at night, usually at 10—20 m. It has a prehensile tail (Mertens 1964a, 1964b; Meier 1979). Near Poindimié and Ponerihouen it occurs in sympatry with *R. chahoua* and with *R. auriculatus, R. sarasinorum* and *R. trachyrhynchus* in southeastern New Caledonia and probably at Mt. Koghis. In all cases except the last it appears that *R. leachianus* is associated with larger trees and higher zones of activity than its congeners. Meier (1979) reported that this species was found most frequently in very large trees which provided numerous holes which provided daytime retreats. Unlike *R. auriculatus*, this species is rather clumsy on the ground, but is a very rapid climber.

Roux (1913) reported that the diet of this species included *Glyciphila (= Lichmera) incana*, a meliphagid bird, one of the only records of a bird as a natural gekkonid prey item. Mertens (1964a) discussed feeding in captivity, emphasizing frugivory and Mitchell (1986) reported captive cannibalism. Nothing is known of courtship in the species but eggs are described by Roux (1913) and Mertens (1964a). *Rhacodactylus leachianus* can inflict a painful bite and when threatened inflates its lungs with air and emits a loud hiss or croak (Bavay 1869; Mertens 1964a).

Rhacodactylus sarasinorum **Roux, 1913 (Fig. 83)**

1913 *Rhacodactylus sarasinorum* Roux. Nova Caledonia, Zoologie I(II): 99; pl. IV (figs. 6,6a).
Type locality: Forêt de Prony (env. 100 m d'altitude), New Caledonia.
Holotype: NMBA 7246.

D i a g n o s i s : No derived character states were found for this taxon in the phylogenetic analysis. However, it may be distinguished from congeners by its gracile form and by the contrasting dark dorsum and cream venter and by its general lack of fleshy folds, digital webbing and bony protruberences.

Fig.83: Holotype of *Rhacodactylus sarasinorum* Roux, 1913. NMBA 7246 (SVL = 110 mm).

C o m m e n t s : All specimens of this species are from extreme southern New Caledonia and are associated with the southern ultramafic formation or outlying areas (Figs. 82,84). This is by far the most gracile New Caledonian *Rhacodactylus* and reaches a SVL of 125 mm (CAS 157675). The specimens examined vary considerably in color pattern and body proportion. Roux (1913) reported the species from leaf litter in a fork of *Pandanus*. I have collected this species 3 m above the ground in a small shrub, approximately two meters away from *R. auriculatus* and within 50 m of a tree containing *R. leachianus*. Böhme & Henkel (1985), Sameit (1985), and Henkel (1987, 1988) described the collection of this species in primary forest and discuss captive care. These publications also present color photographs of the species. Insects and arachnids are the probable wild food of this species (Roux 1913). Mite-pockets have been reported for *R. sarasinorum* (Böhme & Henkel 1985). Infertile eggs have been laid in captivity (Henkel 1986a) and successful capture reproduction has been discussed by Henkel (1987).

Fig.84: Abandoned mining site 8 km south of Goro, New Caledonia. Forest in foreground is typical habitat of *Rhacodactylus sarasinorum, R. auriculatus* and *R. leachianus* (in larger trees). *Bavayia sauvagii* occurs under rocks in adjacent coastal forest. *R. trachyrhynchus* has been collected from similar mountain forest at Gouemba, about 20 km to the north of this site.

Rhacodactylus trachyrhynchus **Bocage, 1873 (Fig. 85)**

1869 *Platydactylus duvaucelii* Bavay. Mém.Soc.Linn. Normandie 15: 6 (nec Duméril & Bibron, 1836 — fide Boulenger 1883).
1873 *Rhacodactylus trachyrhynchus* Bocage. J.Sci.Mat.Phys.Nat. Lisboa 4: 203.
Type locality: Nouvelle Calédonie.
Holotype: MLI (specimen number unknown, destroyed by fire).
1878 *Platydactylus (Rhacodactylus) chahoua* (part) Sauvage. Bull.Soc.Philomat. Paris (7)3: 66.
1878 *Chameleonurus trachycephalus* Boulenger. Bull.Soc.Zool. France 3: 68; pl.2.
Type locality: Ile des Pins (Nouvelle-Calédonie).
Lectotype: IRSNB 2.5 32, here designated.
1879 *Chameleonurus chahoua* (part) Boulenger. Bull.Soc.Zool. France 4: 142.
1883 *Rhacodactylus trachyrhynchus* Boulenger. Proc.Zool.Soc. London 1883: 126; pl. XXI (figs. 2,2a—2d).
1889 *Chamaeleonurus trachycephalus* Carus. Reg.Zool.Anz. 1889: 83.
1913 *Rhacodactylus trachyrhynchus* Roux. Nova Caledonia, Zoologie I(II): 98.

D i a g n o s i s : This species may be diagnosed by the following characters: skin of head co-ossified with skull; two to four inscriptional ribs; rostral excluded from nostril; in-

Fig.85. Juvenile *Rhacodactylus trachyrhynchus* Bocage, 1873. ZFMK 31806. (Photo courtesy of E. Schmidt, Zoologisches Forschungsinstitut und Museum A. Koenig)

fralabials extremely large; first infralabials contact behind mental; digital scansors divided by small central plates; preanal organs do not extend onto thighs; tail long and thick; livebearing; newborns lack egg-teeth. (1, 32-B, **79**, 80, 93-B, 106).

C o m m e n t s : This species was first recorded as *Platydactylus duvaucelii* by Bavay (1869). Bocage's (1873) description is adequate but too brief to be useful. During the subsequent decade Boulenger (1878, 1879), Sauvage (1878), and Bocage (1881) confused this species with *R. chahoua* (Bauer 1985a). The taxonomy of *R. trachyrhynchus* stabilized in 1883 with Boulenger's review of New Caledonian geckos.

This species is currently known from only five confirmed localities, all in central or southern New Caledonia (Fig. 86). An additional record from the Isle of Pines is based on the types of *Chameleonurus trachycephalus* Boulenger, 1878. *Rhacodactylus trachyrhynchus* has been found on bark (Mertens 1964a) and is generally associated with large trees in primary humid forest (Meier 1979; Böhme & Henkel 1985; Sameit 1985). Henkel (1986a) stated that it is a crown-dwelling species, occurring at heights of 20 m or more. The interesting habit of hiding in water-filled bromeliads has been noted in juveniles (Henkel 1986a). Unlike *R. leachianus* this species has a long, stout, prehensile tail. Tail break frequencies are high and may be attributed to predation attempts by raptors, particularly *Accipiter haplochrous* and *A. fasciatus* (Meier 1979). This species reaches a maximum SVL of 170 mm (ZFMK 25398) and in many respects resemble *R. leachianus* in its biology. Wild diet is unknown but probably consists of lizards
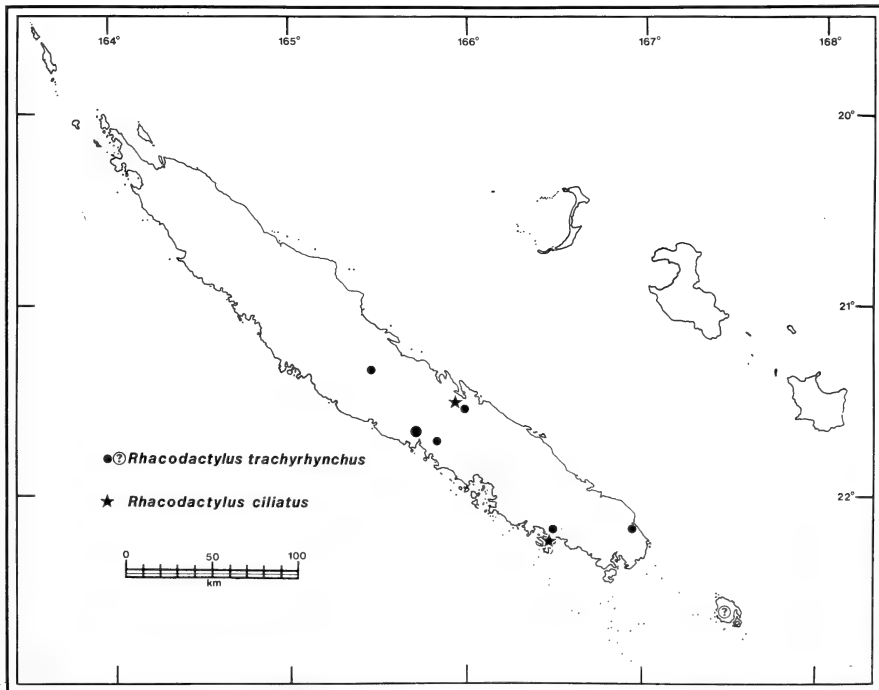

Fig.86: Distribution of *Rhacodactylus trachyrhynchus* and *R. ciliatus* in New Caledonia. Question mark indicates a doubtful record of *R. trachyrhynchus* from the Isles of Pines.

and arthropods. *Rhacodactylus trachyrhynchus* is unique among New Caledonian car-phodactylines in being viviparous (Bartmann & Minuth 1979; Meier 1979). The two young are roughly half the total length of the adult and weigh approximately four grams each (Bartmann & Minuth 1979).

Rhacodactylus (subgenus *Pseudothecadactylus*) (Brongersma, 1936)

1934 *Torresia* Brongersma. Zool.Meded. 17: 176. (non *Torresia* Castelnau, 1875 = Pisces).
Type species: *Thecadactylus australis* Günther, 1877 by original designation.
1936 *Pseudothecadactylus* Brongersma. Zool.Meded. 19:136 (nomen novum pro *Torresia* Brongersma, 1934).
S p e c i e s   r e f e r r e d : *Rhacodactylus (Pseudothecadactylus) australis* (Günther, 1877); *R.(P). cavaticus* (Cogger, 1975); *R.(P). lindneri* (Cogger, 1975).
D i a g n o s i s : (Node 20) A monophyletic subgeneric taxon diagnosed by the follow-ing characters: Five or more abdominal ribs; coracoid process placed posteriorly along interclavicular body; digital scansors present, broadened and divided; digit one of manus and pes clawless; preanal organs (if present) do not extend onto thighs; tail bear-ing subcaudal lamellae. (33, 39, **70**, 74, 76*, **86**, 93-B, 107).

C o m m e n t s : This subgenus is confined to areas of relatively high rainfall in extreme northern Australia. Günther (1877) described *Thecadactylus australis* as the second member of that genus, the only other representative being the neotropical *T. rapicauda*. Although he remarked on the significance of such a disjunct distribution, it was more than sixty years before the two were separated at the generic level. Brongersma (1934) errected *Torresia* for the Australian form and shortly there after replaced this preoc-cupied name with *Pseudothecadactylus* (Brongersma 1936). *Pseudothecadactylus* was placed by Underwood (1954) in the Gekkoninae.

Key to the species of *Rhacodactylus (Pseudothecadactylus)*

1a.Rostral scales approximately as broad as high; ear opening approximately same size as nostril .... *R. australis*
b. Rostral much broader than high; ear opening at least five times size of nostril   2
2a. Rostral excluded from nostril; dorsal body scalation homogeneous . *R. lindneri*
b. Rostral narrowly contacts nostril; dorsal body scalation heterogeneous *R. cavaticus*

Rhacodactylus (Pseudothecadactylus) australis (Günther, 1877) (Fig. 87)

1877 *Thecadactylus australis* Günther. Ann.Mag.Nat.Hist. (4)19: 414.
Type locality: Islands of Torres Strait, Queensland.
Holotype: BMNH 77.3.3.12.
1934 *Torresia australis* Brongersma. Zool.Meded. 17: 176; figs. 5—7.

1936 *Pseudothecadactylus australis* Brongersma. Zool.Meded. 19: 136.
1963 *Thecadactylus australis* Worrell. Reptiles of Australia: 30.
1965 *Pseudothecadactylus australis* Wermuth. Das Tierreich 80: 153.

D i a g n o s i s : 3—4 inscriptional ribs; skin of head co-ossified with skull; lining of mouth and tongue navy to black; first infralabials may contact behind mental; subpygal scales enlarged, hexagonal to octagonal; preanal organs present; ear opening minute; usually one cloacal spur; juvenile color pattern as adult. (1, **62**, 63, 64, 80).

C o m m e n t s : Günther's (1877) description is sketchy. The holotype is from an unspecified island in Torres Strait. Brongersma (1934) provided an excellent redescription and clearly diagnosed *Pseudothecadactylus* as distinct from *Thecadactylus*. The species was known only from the holotype until the discovery of a single individual from the McIlwraith Ranges (Loveridge 1934). The species is now known to range throughout the northern Cape York Peninsula and Islands of Torres Straits (Fig. 25) and it possibly occurs on the mainland of New Guinea. Worrell (1963), in his discussion of *"Thecadactylus australis"*, seems to have confused this species with its ex-congener *(T. rapicauda)*, including tropical America as well as northern Queensland in its range.

Fig.87: Holotype of *Thecadactylus australis* Günther, 1877 (= *Rhacodactylus australis*). BMNH 77.3.3.12. (Photo courtesy British Museum (Natural History))

Rhacodactylus australis reaches a maximum SVL of 120 mm (Cogger 1986 — largest specimen measured by author 112 mm QM J38327). It is chiefly arboreal and its habitat has been described as woodland and open forest (Cogger et al. 1983) heaths, monsoon forest, woodland and mangrove (Covacevich & Ingram 1980). Specimens have been collected in hollows of *Melaleuca cajuputi* (Cogger 1975). It is primarily an arthropod feeder.

Rhacodactylus (Pseudothecadactylus) cavaticus Cogger, 1975

1975 *Pseudothecadactylus lindneri cavaticus* Cogger. Rec.Aust.Mus. 30: 93; figs. 5—6.
Type locality: near Mitchell River Falls, approx. 25 km SW of Crystal Head, Port Warrender (approx. 14°40'S, 125°42'E), Western Australia.
Holotype: WAM R43176.

D i a g n o s i s : No inscriptional ribs; no co-ossification of skull; mouth and tongue pink in life; ear opening large; dorsal scalation heterogeneous; preanal pores absent; dorsum with broad light bands with lighter centers. **(78, 92)**.

C o m m e n t s : *Rhacodactylus cavaticus* is known only from the coastal region of the Kimberleys, W.A. (Fig. 89) where it occurs in association with caves and crevices of sandstone formations (Cogger 1983). I have not examined specimens of this form but consistent differences in morphology suggested by the description (Cogger 1975a) seem to warrent the recognition of this taxon at the specific level.

Rhacodactylus (Pseudothecadactylus) lindneri Cogger, 1975 (Fig. 88)

1975 *Pseudothecadactylus lindneri* Cogger. Rec.Aust.Mus. 30: 89; figs. 1—5.
Type locality: Deaf Adder Gorge, Arnhem Land, Northern Territory.
Holotype: AMS R38734.

Fig.88: Holotype of *Pseudothecadactylus lindneri* Cogger, 1975 (= *Rhacodactylus lindneri*). AMS R38734. (Photo courtesy of The Australian Museum)
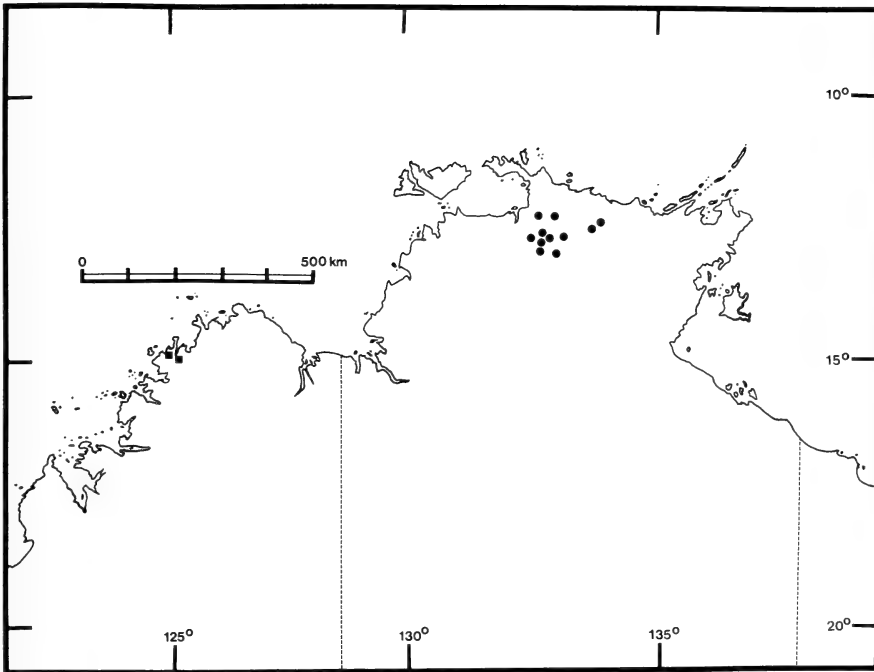
Fig.89: Distribution of *Rhacodactylus lindneri* (circles) and *R. cavaticus* (squares) in northern Australia.

D i a g n o s i s : No inscriptional ribs; no co-ossification of skull; mouth and tongue pink in life; ear opening large; dorsal scalation homogeneous; preanal pores greatly reduced; dorsum with narrow light bands, fading laterally to spots.

C o m m e n t s : *Rhacodactylus lindneri* is a large gecko (maximum SVL 107 — Cogger 1975a) which went undiscovered until 1972. Cogger's (1975a) description and diagnosis of the species is complete and informative. It is endemic to western Arnhem Land, N.T. (Fig. 89) where it is found in association with sandstone formations (Cogger 1975a, 1981) (Fig. 90). Cogger (1975a) discussed and illustrated the moderately prehensile scansorial caudal pad of *R. lindneri*. It feeds on spiders and insects as well as members of the genus *Gehyra* which co-occur on sandstone faces. This species at East Alligator typically becomes active about three hours after sunset and will frequently leap from the rock faces of the sandstone escarpments to nearby trees where they will forage for several hours before returning to refuges in the rock walls (pers. obs.).
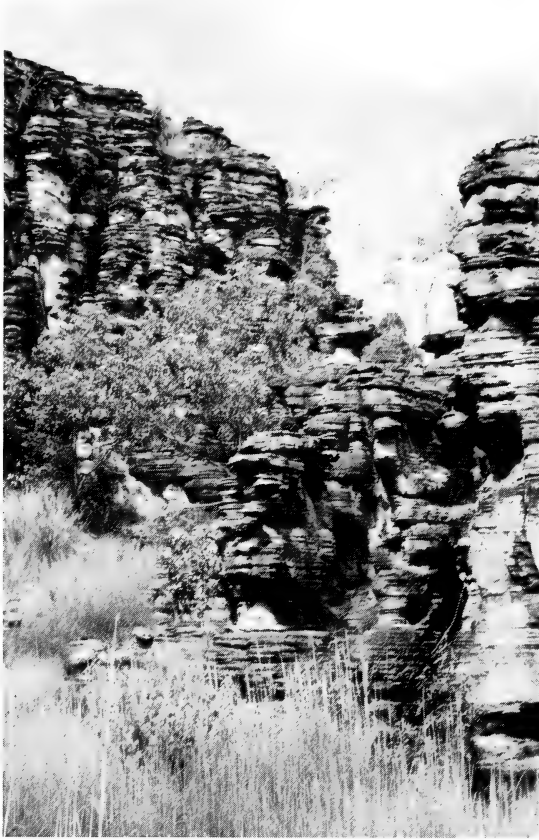
Fig.90: Sandstone outliers at the western edge of the Arnhem Land Escarpment, Ngarragji Warde Djobkeng, near East Alligator Station, Kakadu National Park, Northern Territory, Australia — typical habitat of *Rhacodactylus lindneri*.

ACKNOWLEDGMENTS

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APPENDIX A

Collection Acronyms. Alcoholic, skeletal or living specimens from the following gekkonid collections have been examined or referenced in this study. For complete addresses of most institutions see Leviton et al. (1985). Institutions marked with an asterisk no longer exist.

AIM — Auckland Institute and Museum (Auckland, New Zealand)

AMB — Aaron M. Bauer, personal collection (Villanova, U.S.A.) (to be deposited in the collections of CAS and MVZ)

AMNH — American Museum of Natural History (New York, U.S.A.)

AMS — The Australian Museum (Sydney, Australia)
ANWC — Australian National Wildlife Collection (Canberra, Australia)
BMNH — British Museum (Natural History) (London, England)
CAS — California Academy of Sciences (San Francisco, U.S.A.)
CAS/SU — California Academy of Sciences/Stanford University Collection (San Francisco, U.S.A.)
CMC — Canterbury Museum (Christchurch, New Zealand)
EMNB* — Musée de l'école de Médecine Navale (Brest, France)
FMNH — Field Museum of Natural History (Chicago, U.S.A.)
IRSNB — Institut Royal des Sciences Naturelles de Belgique (Brussels, Belgium)
LACM — Los Angeles County Museum of Natural History (Los Angeles, U.S.A.)
MCZ — Museum of Comparative Zoology, Harvard University (Cambridge, U.S.A.)
MHNG — Muséum d'Histoire Naturelle (Génève, Switzerland)
MLI* — Museu de Lisboa (Lisbon, Portugal)
MMNH — Musée d'Histoire Naturelle (Marseille, France)
MNHN — Muséum National d'Histoire Naturelle (Paris, France)
MNNZ — Nelson Museum (Nelson, New Zealand)
MVZ — Museum of Vertebrate Zoology, University of California (Berkeley, U.S.A.)
NHMG — Naturhistoriska Riksmuseet (Göteborg, Sweden)
NHRM — Naturhistoriska Riksmuseet (Stockholm, Sweden)
NHW — Naturhistorisches Museum (Wien, Austria)
NMBA — Naturhistorisches Museum Basel (Basel, Switzerland)
NMNZ — National Museum of New Zealand (Wellington, New Zealand)
NTM — Northern Territory Museum of Arts and Sciences (Darwin, Australia)
PFN — Parc Forestier (Nouméa, New Caledonia)
QM — Queensland Museum (Brisbane, Australia)
RMNH — Rijksmuseum van Natuurlijke Historie (Leiden, The Netherlands)
SAMA — South Australian Museum (Adelaide, Australia)
SMF — Natur-Museum und Forschungs-Institut Senckenberg (Frankfurt-am-Main, Federal Republic of Germany)
SMNS — Staatliche Museum für Naturkunde in Stuttgart (Ludwigsburg, Federal Republic of Germany)
UMMZ — University of Michigan Museum of Zoology (Ann Arbor, U.S.A.)
USNM — United States National Museum of Natural History (Washington, U.S.A.)
WAM — Western Australian Museum (Perth, Australia)
ZFMK — Zoologisches Forschungsinstitut und Museum Alexander Koenig (Bonn, Federal Republic of Germany)
ZMA — Universiteit van Amsterdam (Amsterdam, The Netherlands)
ZMB — Universität Humboldt (East Berlin, German Democratic Republic)
ZMH — Universität Hamburg (Hamburg, Federal Republic of Germany)
ZMUC — Kobenhavns Universitet (Copenhagen, Denmark)
ZMUZ — Universität Zürich (Zurich, Switzerland)
ZSM — Zoologische Sammlung der Bayerischen Staates (München, Federal Republic of Germany)

APPENDIX B

Specimens Examined (for acronyms see Appendix A). An asterisk following a specimen indicates a holotype, neotype or lectotype. Type specimens associated with junior synonyms are not indicated here but are listed under the appropriate species in the species accounts. Unless otherwise indicated all specimens are alcohol preserved. (s) = dry skeletal preparation, (c+s) = cleared and stained preparation. In addition to specimens listed most taxa have been observed alive.

Bavayia crassicollis (17 specimens):
CAS 157695; MCZ 19633, 27935; NMBA 6931*, 6933-41; USNM 146331-2; ZFMK 30548, 32652.

Bavayia cyclura (200 specimens):
AMNH 24681-83, 60472, 61683-7, 61689-91, 81758, 81768, 81772; BMNH 71.4.16.30* (A-B), 85.11.16.15-16, 86.3.11.11-15, 1926.9.17.8-19; CAS 80864-8, 80869 (s), 80870-71, 157696-704, 158548-50, 159546, 159550-1, 162203-9, 162219-21, 162237-9; 165861-74; 165877-79; 165884-7; FMNH 25921, 105666-7, 105710, 170762; MCZ 6209, 9293-4, 29935, 162911; MNHN 703 (A-E), 5310-1, 5790, 85.24, 85.755, 88.82, 1980.977-9, 1980.1063-6, 1981.172-3, 1985.112-19; NMBA 2901-4, 6894-6, 6898-912, 6915, 6917-21, 6923, 6925-6, 6929-30; NMW 19362 (2-5); RMNH 6788-9; SMF 9029, 9121; UMMZ 64306, 93830 (1-9), 93831, 93832 (0-10), 93833, 127507(c+s), 174097; ZFMK 15895, 25404-5, 25448.

Bavayia montana (23 specimens):
CAS 157694; MCZ 19634; NMBA 6942-45, 6946*, 6948-56, 6959; USNM 267840-1; ZFMK 25402-3, 25447, 48663.

Bavayia ornata (15 specimens):
AMS R77843, R77870-4, R77888, R77892-3; NMBA 7023, 7024*, 7025-8.

Bavayia sauvagii (418 specimens):
AMNH 24689-90, 60469-71, 61589, 81769-71; AMS R6678, R64917, R77543-4, R77660-4, R77687, R77721, R77782, R77801-4, R77815-6, R77844-6, R77859, R78350-2; BMNH 71.4.16.31* (A-C), 1926.9.17.2; CAS 38826, 80823(s), 80824-63, 157705-10, 157711-8, 157914-70, 158321-32, 158378-83, 158386-8, 158430-508, 15913-25, 159528-43, 159552-3, 159555-61, 159566-7, 162184-200, 162213-8, 162225, 162228-32, 162235, 162240-3, 165875-6, 165880-83, 165888-9, 165893-4 (s), 165903-10 (c+s); FMNH 62804-5, 106963-4; MCZ 19635, 27938, 46171; MNHN 5312; NHRM AAA/1912809.3733; NMBA 6981-5, 6987-99, 7001-7, 7009-10, 7012, 7014-6, 7018-22; NMW 14754, 19362 (1), 19363 (1-2), 19366 (1-2), 19672 (1-2); RMNH 6787; SMF 9030; UMMZ 64307-8, 174469; USNM 59008-9, 267842, 268761; ZFMK 16102-12.

Bavayia septuiclavis (16 specimens):
AMS R78139*41, R782346, R78339, R90193, R125888, R125291-3; MNHN 1985-120, 1985-121; ZFMK 25400, 45032-4.

Bavayia validiclavis (10 specimens):
AMS R77353, R77847, R77853-4, R77855*, R77856-8, R77895; MNHN 1980-1067.

Carphodactylus laevis (38 specimens examined):
AMNH 69530, 83857; AMS R2252, R10095, R10835-46, R10847(c+s), R11377-81, R55938, R56335-6, R58304, R64914; BMNH 1960.1.5.70; FMNH 57492; MCZ 35109-12, 35114-5; RMNH 6407(1-2); SMF 22504.

Eurydactylodes symmetricus (6 specimens):
MNHN 94.453, 94.454, 94.454a, 1985.123; NHMG 651*; NMBA 7072.

Eurydactylodes vieillardi (22 specimens):
BMNH 90.7.26.1, 1926.4.17.7, 1927.11.22.1; CAS 158556; MNHN 5313, 699-1863; NHMG 605; NMBA 7068-71, 9703; UMMZ 174095-6; USNM 267843; ZFMK 16113, 46981*, 48259-62, 48981.

Hoplodactylus chrysosireticus (13 specimens):
AIM J257-8, J779-81, 841(s); CMC 512, 543; NMNZ R25*, R1857, R1867, G559, G923.

Hoplodactylus delcourti (1 specimen):
MMNH 1985-38* (skin and partial skeleton).

Hoplodactylus duvaucelii (138 specimens):
AIM 162-9, 666-7, 717, 884(s); AMB 455(s); AMS R114880; BMNH 45.2.15.81, 61.3.20.11(s); CMC 180, 224; FMNH 207824, 210144; MCZ 18413; MHNG 653.82(1-2); MNHN 5977*, 6680*1*; NMNZ G4-6, G91-2, G118, G128, G134-6, G141-4, G147-50, G219, G358-9, G366-71, G384, G476, G505, G569-70, G581, G583-6, G597-600, G606-7, G609-10, G624-5, G627, G631-2, G641, G643, G651, G654-5, G667-8, G705-6, G708-9, G712, G719, G723, G731, G747, G753-6, G761, G794, G808-9, G850-3, G860-1, G895, G966-72, G1009-12, G1088-9; NMW 20808(1-7); RMNH 2722*; SMF 9036-7; SMNS 184a-b; UMMZ 127158(1-2), 129351; USNM 209587; ZMH R02822-3.

Hoplodactylus granulatus (104 specimens):
AIM 235-49, 668, 673(s), 703-14, 735-741, 754, 888(s), 919-20(s); AMB 450, 451(s); AMNH 22407, 68920; AMS R427, R1320, R1660, R4458-9, R5216, R5233; BMNH 1946.8.22.71*; CAS 47982-3, 47984(s), 47985, 47987; CMC 160, 182-3, 185-7, 189-91, 205, 208, 219, 256; FMNH 18180; MNHN 33:131-3; NMNZ R51-2, R56-9, R93, R459, R1047, R1752; NMW 17920; RMNH 2500; SMF 9038; SMI E81.4; SMNS 186a-b, 187; USNM 209588-9; ZFMK 30055, 37310-1, 40177; ZMH R02821; ZMK R34729-33.

Hoplodactylus kahutarae (4 specimens):
NMNZ R1980*2, G345.

Hoplodactylus maculatus (151 specimens):
AIM 545-9, 745-60, 842, 928, 935(s), 938(s), 944(s), 952(s), 960(s), 990(s); AMB 88(s), 89-90, 91(s), 92,93(living), 94-5; AMNH 22408-16, 23058, 31547(s), 65539; AMS R3820, R4460-2, R5578, R12073 (1-4); BMNH 1946.9.8.14-15*; CAS/SU 12211-15; CMC 172, 176, 179, 184, 200-4, 206, 212, 216-8, 225-6, 228, 233, 257, 260, 262-3, (two specimens - no catalogue number); MCZ 6153, 28653, 126223-6, 152218; MHNG 653.84(A-B), 661.80(A-B), 678.30(A-B); MNHN 6684; MVZ 187689; NMBA 2906-8, 21324; NMW 17921 (1-4), 20762; RMNH 4442(1-2);SMF 9034-5, 50612-5; UMMZ 127126-7, 129366; USNM 209590-1; ZFMK 26270-1, 37305-9; ZIH 4778, 6341, 6391, 10380(1-2), 29025(1-3); ZMH R02819-20; ZMK R34219-22; R34725-8.

Hoplodactylus pacificus (229 specimens):
AIM 188-234, 615, 676-7(s), 734, 761-72, 774-5, 777, 785, 795-6, 803-5, 808, 838, 846-8, 933(s), 939(s), 942(s), 946-7(s), 956(s); AMB 481(s), 482 (c+s); AMNH 31536-50; AMS R4457; BMNH 62.9.2.18(s), 1946.8.22.64*, 1946.8.22.65-6; CAS 47975, 47978-81; CMC 181; FMNH 58146-87; MCZ (three specimens - no catalogue number); MNHN 33:13h, 6465, 6682-3, 6685-6; NMW 14750(1-2)(?), 14751, 17922(1-14), 17923(1-19), 17924(1-6), 17925(1-22), 20416; 4442(1-2), 4443(2); UMMZ 54110(1-2), 60483; USNM 5690; ZFMK 30056-7; ZIH 7621(1-2), 13839, 18762-3.

Hoplodactylus rakiurae (6 specimens):
NMNZ R1823-5*, R2014, R2043, G236.

Hoplodactylus stephensi (9 specimens):
CAS 47986; NMNZ 163-4, R1061, R1857-1858*, R1859-61.

Naultinus elegans (131 specimens examined):
AIM 360-74, 742-7, 791-2, 890(s), 912(s), 929(s), 934(s), 940(s), 943(s), 949, 992; AMB 394-395(c+s), 480; AMS R4454, R4456, R5239, R5378; BMNH 1975.854(s); CAS 47776-7; CMC 174, 178, 181A, 188, 192, 198, 244, 277, 534-6, 541-2, 557, 560; FMNH 18179; MNHN 5007, 6750-2 NHNG 661.78(A-B), 661.79; NMBA 231-2, 2905, 19650, 21325; NMNZ R75-6, R78-81, R915; NMW 14980, 17918(1-8), 17919(1-13); RMNH 4445; SMF 9031-3, 69410, 69416, 69419; SMNS 175; SNMR NNN/1928989.6451; UMMZ 127576(1-2), 142536(c+s) 192352(1-2); ZFMK 37313-6; ZIH 5188, 7832, 8195, 10381, 15557, 18764-5; ZMH R02824; ZMK R34120-3, R34734, R34736-7.

Naultinus gemmeus (80 specimens examined):
AIM 719-22; AMNH 22406, 23059-60; AMS R4455, R12264; BMNH 72.10.14.8-10; CMC 173, 175, 177, 213, 250, 276, 339, 523-6, 527(1-4), 528-30, 531(1-2), 532, 538, 540, 545, 550; MHNG 653.83; NMNZ R1870-2, R1875-6, G129-30, G233-5, G413-6, G516, G790, G857, G879, G896, G898, G902, G905, G936, G1070, G1092, G1098-103; SMF 69414; SMI E81.5, 83.3356; SMNS 174a-b; UMMZ 129356-7, 142538(s); ZIH 7875, 13838; ZMH R02825.

Naultinus grayii (24 specimens examined):
AIM 551-2, 786-7, 789(1-2), 889, 891(s), 892(s), 893(s), 894(s), 937(s); CMC 514(1-2), 537, 554-6, 558-9(s), 561; ZIH 8195; ZMH R02826; ZMK 34735.

Naultinus manukanus (22 specimens):
AIM 725-7; NMNZ R238*, R448, R2008, R2012-3,G2, G54, G99, G122, G125, G127, G137, G312-3, G437, G517, G528, G798, G939.

Naultinus poecilochloris (6 specimens):
NMNZ R1863-6, R1992, G1064.

Naultinus rudis (18 specimens examined):
BMNH 86.5.15.40 (1946.8.22.37)*; CMC 513, 515; NMNZ R1817, G485, G791, G799, G854-6, G900-1, G1057-62.

Naultinus stellatus (67 specimens examined):
AIM 723-4; AMB 483; BMNH 1905.11.30.9; CMC 518-22, 539; NMNZ R2002-4, R2006, G12-8, G33, G346, G421, G429, G440, G442, G471, G504, G509-10, G529-30, G792, G796, G800, G858, G878, G903, 1056, G1067-9, G1071, G1079-83, G1091, G1093-7; SMF 69411-13; UMMZ 129353-5, 132102, 142539(1-5)(c+s).

Naultinus tuberculatus (8 specimens examined):
AIM 718; CMC 171, 199, 516-7; NMNZ G208, G1072; UMMZ 127571 (c+s).

Nephrurus asper (68 specimens examined):
AMNH 5086, 27317, 27324, 86395-7; AMS R1131(c+s), R1883, R1925(1-2), R10371, R10905(c+s), R11965, R12876, R13403, R14183, R15107, R20449-50(c+s), R31773, R40070, R42760, R49716, R50542, R55786, R63065, R72980, R88668, R90198, R93181-2, R104458, R107165, R107703, R110544, R110562, R113116, R113852, R120094, (one specimen, no number) ; BMNH 76.3.4.5, 1926.2.25.20, 1946.8.23.34*; CAS 74732-5, 76250, 77509; MCZ 13961-2, 83257; NMW 17267; SMF 8139, 61685, 61745, 69297-9; SMNH MJO/1910484.5978; ZFMK 42040, 42506, 44665, 46992-4; Z1H 10773-4.

Nephrurus deleani (10 specimens examined):
AMB 45, 46(s), 47-8, 49(s); SAM R21864-8*.

Nephrurus laevissimus (50 specimens examined):
AMS R17585, R49672, R49680, R49730, R49736, R86506-7, R91077-81, R100910; BMNH 1957.1.10.34, 1969.2403-10; FMNH 97652; LACM 57065, 57071, 57080, 57086, 57090, 57092(c+s), 57101(c+s), 57117, 57120, 57140; MCZ 158551-2; SAM R665(c+s), R15566B, R18221; SMF 53201*; ZFMK 42036-9, 42511-2, 43678, 45955-7; 46420.

Nephrurus levis (189 specimens examined):
AMNH 24922-5, 62882, 86393, 86394(c+s); AMS R2039, R2105(c+s), R2407, R5397, R6754, R6917, R7672, R7693, R10905-6, R11400(c+s), R11966-7, R13028, R13403, R13941-2, R14338, R16471, R17741, R20451-2(c+s), R20845, R21217, R27936, R31593-4, R31648, R31774, R32397, R32909, R40457, R41674, R47529, R49084, R49091, R49801, R49529, R49581, R49673, R49681, R49692-3, R49718-9,R49735, R50666, R50674-6, R52138-41, R55787, R55992, R56949, R57097-8, R60282, R65100, R65287, R66651, R70039, R70049-50, R73915, R76644, R83250-72, R86499, R93002, R95426, R96111-3, R96126, R96130-1, R96160, R101551-2, R101580, R101785-7, R101981, R102446-58, R102519, R102546-7, R102599-610, R105641, R105700, R105729, R105762, R110578, R110594, R113264-73, R114829-30; CAS/SU 12610; FMNH 95840, 202409; LACM 57010, 57019, 57035-6; MCZ 28654, 43113, 74997, 78673-4, 79447, 163948; MVZ 78122, 78827; NMW 17263-5, 17266 (1-2); SMF 8140-2, 69306-7, 70181; SMNH MJO/1911809.5979; ZFMK 25380-1, 42035, 45024, 45380, 45952-53, 46419; ZIH 29655; ZMH R02829.

Nephrurus milii (338 specimens examined):
AMB 460(s), 499; AMNH 50585(c+s); AMS R44, R53, R97, R231, R254, R1047, R1942, R1969, R2426, R2465, R2481, R2691, R2951, R3115, R3409, R3412, R3417, R3427, R3435, R3595-6, R3868, R3875, R4412, R4566 (1-2), R4567, R4584-5, R4923-4, R5293, R5310, R6089-90, R6116, R6259, R7144, R7177 (1-3), R7670-1, R7725, R8375-6, R9136, R9448, R10033, R10059, R10465, R10550, R10986, R11149, R11718 (1-2), R12205-6, R12413, R12577, R13128, R14642, R14993-4, R15104, R15206, R15577, R15862-3, R16118, R16972, R17187, R17856-61, R18479, R18645, R18662, R18681-3, R18732, R18777, R19259, R20353, R20534, R20561, R26031, R26187, R26504-5, R27327-8, R27348, R27799, R28066, R28546, R29702-3, R39505-6, R40118, R40422, R41201, R42716, R44721, R45328-62, R50672-3, R54079-80, R55812-20, R61518-21, R64942, R66243, R67656-8, R68315, R69205-6, R69718, R69841-62, R70038, R70042, R70130, R76711-2, R81385, R81540-2, R81763, R86212-3, R86332-7, R86491-2, R89140, R89219-21, R93815, R93922, R93924, R93929-31, R94644, R94833, R94837, R95851, R97919, R99367, R101967-8, R102611-9, R103560, R103717, R104822, R105614, R105788, R106612-3, R106940, R107697, R107914, R107919-22, R108909, R111051, R111952, R113125, R114262, R114479, R114553, R115227, R115667, R115740-3, R115788, R120572; BMNH 55.10.16.106(s), 1913.7.28.1, sixteen specimens (no numbers); CAS 74743-5, 83634(c+s), 83635, 94188-9, 100887-90, 100923-4; MNHN 2334-5, 5318, 5601; NMBA 2665, 18104-5; NMW 17423(1-2), 17424(1-2), 17425-7, 17428(1-4); RMNH 2636(1-3), 2637; RSW (2 specimens, no numbers); SMF 21667, 40008, 45418, 66197; USNM 6479, 58909, 62732-3, 63126, 63167-9.

Nephrurus sphyrurus (23 specimens):
AMS R1818, R2766, R2768, R3800*, R4880, R5617, R6770, R6771(c+s), R6772-3, R10266, R10532, R12571, R15195, R15642, R35188, R51688-9, R69717, R106935; BMNH 1912.11.1.89; QM J3859, J4342.

Nephrurus stellatus (4 specimens examined):
SAM R18515; ZFMK 48263-4; ZIH 02828.

Nephrurus vertebralis (5 specimens examined):
AMS R96161-2; LACM 57044, 57048; RMNH one specimen (no number).

Nephrurus wheeleri (12 specimens examined):
AMS R100897, R100899; BMNH 1932.7.13.1, 1946.8.23.52; MCZ 32950*3; RMNH 6406; SAM R222, R4485; ZMH R02827.

Phyllurus caudianulatus (100 specimens examined):
AMNH 27326; AMS R20427(c+s), R47521, R47551-6, R47641, R47654-7, R47738-62, R47836-49, R47888, R47896, R47901-14, R47956-7, R47959, R57782, R57912, R61473, R76186, R90205, (19 specimens, no numbers); QM J15619*, J22286-7, J24132, J25411.

Phyllurus cornutus (112 specimens):
AMNH 20876, 27261, 27302, 27325, 69534-5, 120292-3; AMS A233, R748, R749*, R750, R752-3, R1094, R2315, R2409, R3795, R3799, R4769, R5839, R6247, R6284, R6792, R6915, R8103, R8253, R11160, R11375, R11553, R11621, R11844, R12935, R15412, R16905, R16989, R17008, R20447-8(c+s), R26117-23, R41148, R42163, R43870-7, R47494, R54071, R55810-1, R59313-4, R65251-2, R69866-7, R70058-9, R71372-3, R81921, R92119-23, R97670-2, R97823, R98332-3, R101338, R103031, R106749, R110510, R116978; BMNH 1963.592-3; CAS 44119, 44120(s), 44121-23, 44135; FMNH 29046, 35237, 37495-503, 97699; NMW 17440; SMF 22502; USNM 64947-9; ZFMK 29114.

Phyllurus platurus (288 specimens examined):
AMB 42(s), 43-44, 1453(s), 1454 (c+s), one specimen, (no number) (c+s); AMNH 12858(c+s), 20875, 32873-4, 44940, 97748, 121268; AMS A1237, A9615, 4942, 5241, R959, R966, R992, R1124, R1550, R1575, R2306, R2531, R3134, R3182, R3392, R3582-3, R3585, R3588, R3601, R3666, R3793, R4396, R4404, R4814, R5181-2, R5520, R6141, R6728, R7189, R7194, R7294, R7747, R7987, R8018, R8037, R8087, R8125-6, R8271, R8277, R8595, R8980, R9274, R9305, R9826, R10051, R10066, R10068, R10220, R10374, R10377, R10384, R10387, R10412, R10429, R10482, R10504, R10761, R11587, R11701, R11753, R12209, R12907, R13105, R16117, R19084, R20381, R20419-20(c+s), R21047, R25891, R25912, R26208, R27324-5, R27330, R27334, R27740, R28308, R32613, R47958, R49185, R51776, R55802-9, R58269, R60995, R61097, R68314, R68342, R69814-40, R69865, R69870-94, R70051-4, R70128-9, R74914, R76444, R80742, R81912-20, R81922, R92870, R93900, R93997-8, R97261-2, R103126-8, R106491-9, R106601-11, R106801, R107089, R110651, R110701, R110762, R110889, R121020, nineteen specimens (no numbers); FMNH 29047, 75163-4, 97697-8, 207638, 207821, 213244; NMBA 2666-7, 8001-3; NMK R34118, R34740-1; NMW 14737(1-6), 14739(1-3); SMF 61215, 61216(1-10), 65242, 68269; SMNS 4466; USNM 5679, 5890-1; ZFMK 20560-2, 30903, 38646; ZIH 5127, 5204, 8530, 46662.

Phyllurus salebrosus (33 specimens):
AMS R300, R5586, R5838, R47884; CAS 74737-42; QM J2879, J8142, J4474, J4897, J5390, J6198, J6382, J8377, J9770, J22288 J25360, J28741, J28802, J29778, J33700, J33730-2, J33744, J35400, J35448, J36114, J36116.

Rhacodactylus auriculatus (137 specimens):
AIM 926; AMS R78113-25, R78126-7, R78232-8, R78304-8, R90186-7, R93711; BMNH 85.11.16.2-4, 86.3.11.5-9, 1926.9.17.5; CAS 157676-84, 158389-90, 158919-25, 159512, 162178-83, 165858-60, 165891-2(s), 165895-902(c+s); MCZ 15968; MNHN 5305, 5305a, 86.393-5, 87.272-5,

94.450-1, 1974.804-5, 1985.108-9; NHMG 874 (1-3), 658 (1-11); NMBA 2909, 7047-8, 7050-2; NMW 17926 (1-4), 18609; RMNH 5451; SMF 61778, 64806, 71024; UMMZ 127599(c + s), 174094; ZFMK 29111, 38940, 43584, 43685-9, 45036, 45384, 46119; ZMH R02830.

Rhacodactylus australis (39 specimens examined):
AMS R38502, R46293-6, R46415, R48089, R57783, R59951, R61974-5, R62332, R64236-7, R76618, R82597, R91493-4, R91496, R93651, R94466, R99835, R99973, R106907; BMNH 77.3.3.12*; MCZ 35162, 45502; NMW 17426; QM J6433, J8164, J28785, J29126, J30064, J31823, J38220, J38327, J38332, UMMZ 127150, 127598(c + s).

Rhacodactylus chahoua (13 specimens examined):
CAS 156691-2*(neotype), 162177, 167764(s); NMBA 9702; SMF 61779; ZFMK 27653, 30549, 38631-4, 42410.

Rhacodactylus ciliatus (16 specimens examined):
BMNH 85.11.16.5-6, 85.11.16.7(s), 90.7.26.2-3,3a-b; IRSNB 797; MNHN 701*, 701a*, 1312, 1755, 4213, 1974.802; NMW 17927 (1-2).

Rhacodactylus leachianus (47 specimens examined):
AMNH 62686; AMS R90386; BMNH 53.8.16.13, 85.11.16.1, 86.3.17.1, 1926.9.17.6; CAS 80879-81, 156690, 159510, 165857, 165890(s); IRSNB 806; MCZ 15967; MMNH (1 spec. no number); MNHN 702, 1483, 4210, 6687*, 86.24; NHMG 657 (1-2); NMBA 7053, 7057-60, 7062, 7064-7, 7095; NMW 17668, 17928; SMF 59030-1, 60655, 65887; USNM 267945; ZFMK 2539, 36270, 45845, 46983; ZMH R02831.

Rhacodactylus lindneri (42 specimens examined):
AMS R37128(c + s), R37129-33, R38730-3, R38734*, R38735, R38945-6, R39493, R39496-7, R39520-2, R39895, R39975, R39992, R40283, R41843-4(c + s), R42123, R75697-700, R76506, R88616, R90194-5, R97346; MVZ 99554; ZFMK 25506-9, 38640.

Rhacodactylus sarasinorum (8 specimens examined):
AMS R90188; CAS 157675; MNHN 94.452*; NMBA 7246*; ZFMK 46408, 46984-6.

Rhacodactylus trachyrhynchus (31 specimens examined):
Alcoholic specimens - AMS R78129-32, R90185; BMNH 80.6.17.5a-b, 86.3.11.2-3, 86.3.11.4(s), 1920.1.20.305; IRSNB 2.532, 786s; MCZ 19647; MNHN 700, 5789, 85.756, 86.271-2, 1974.803; NMBA 7039-42, 7044, 7046; ZFMK 25398; 29112, 31806, 46106, 46982.

APPENDIX C

Character Matrix (all characters for all carphodactyline taxa). Missing data are represented by a 9. Character numbers refer to the character state descriptions in the text. Character states entered as unpolarized are listed as letters. Polarized characters are listed as numbers.

Characters

```
                    1111111111222222222233333333334444444444555555555566666666667777777777888888888899999999990000000000 1111111
          1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890123456789 1234567

Taxon
```

Taxon	Character data
Bavayia cyclura	00000000B000AB0A00001001A00009ABAB00000B000A00000B000B0010A00AAA09000000111B00BABA090A00100000A1B0101
Bavayia sauvagii	00000000B000AB0A0001001A00009ABAB00000B000A00000B000B0010A00AAA09000000111A00BABA090A00100000A0B0101
Carphodactylus laevis	11101011A010AA0B1110110A1011BBABA00100A111A0100011A019A0000A00AAA09011000099000ABBA1A0A0100000A1A0A0009
Eurydactylodes symmetricus	00000000B000AB1A0000011A00009AACB00000A000A00000B00BB0010A00AAA09000000110900AAA090A1010100A0A0000A0B1101
Eurydactylodes vieillardii	00000000B000AB1A0000011A00009AACB00000A000A00000B00BB0010A00AAA09000000110900AAA090A1010100A0A0000A0B1101
Hoplodactylus chrysosireticus	09999999999999990999999990AA9999999999099999990999990BB0010B00BAAA090A00100000A0A0000A0B011
Hoplodactylus delcourti	00010008000BA1A00000001A00009A9999999999999990BB0010B00BAAA090A00100000A0B0099
Hoplodactylus duvaucelii	00010008000BA1A00000001A00009ABAB00000A000A00000B00BB0010B00BAAA090A00100000A0B0011
Hoplodactylus granulatus	00000000B000BA1A00000001A00009AABB00000A000A00000B00BB0010B00BAAA090A00100000A0B0011
Hoplodactylus kahutarae	09999999999999990999999990AA0AB00000A000A00000B00BB0010B00BAAA090A00100000A0A0000A1B011
Hoplodactylus maculatus	00000000B000BA1A00000001A00009ABAB00000A000A00000B00BB0010B00BAAA090A00100000A0B0011
Hoplodactylus pacificus	00000000B000BA1A00000001A00009ABAB00000A000A00000B00BB0010B00BAAA090A00100000A0B0011
Hoplodactylus rakiurae	00000000B000BA9A00000001A00009AAAA00000A000A00000B00BB0010B00BAAA090A00100000A0B0011
Hoplodactylus stephensi	00000000B000BA1A00000001A0001AAABB01000A0AA000000B00AB0010B00BAAA090A00000000A0A0010
Naultinus elegans	00000000B000AA1A001001A0001A0001AAAB0A1000A000AA110A011A0A0000A0A0000A0A0000A0A0010
Naultinus gemmeus	00000000AA9AA001000100A00001AAABA00A0A0000A00000B010BB10001BB100001B000100000A0A0010
Naultinus grayii	00000000AA9AA001000100A0001AAABA00A0A0000B010BB10001BB100001B0000A0000A0A0010
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Naultinus poecilochloris	00000000AA9A00010001A0001AAABB10000A000A00000B00AB0010B00AAAA090A00000000A0A0010
Naultinus rudis	00000000AA9A00010001A0001AAABB10000A000A00000B00AB0010B00AAAA090A00000000A0A0010
Naultinus stellatus	00000000B000AA9A00010001A0001AAABB10000A000A00000B010B00AAAA090A00000000A0A0010
Naultinus tuberculatus	09999999999999991909999909991AA9999999999999090999B00AB0010B00ABAA090A00000000A0A0010
Nephrurus asper	01010011A010AA0B1110000B111BAAAA10100A110B101001A110AA110001A0AA090110199990191099B0A0000
Nephrurus deleani	01010011A010AA0B1110000B111BAAAA10100A110B102001A10AA0A0110199901AAB1A0B000000191101111B0A0000
Nephrurus laevissimus	01010011A000AA0B1110000B111BAAAA10100A110B12001A10AA1100A0110199901ABAB1A0B000000191101111B0A0000
Nephrurus levis	11010011A000AA0B1110000B011BAAAA10100A110B10201A10AA1100A0110199901ABAB1A0B1000001191101111B0A0000
Nephrurus milii	01000001A000AA1B111010B0110B00A1B00001A00001A000A00AA0000A0090110099900AAAA1A1A010000191101100B0A0000
Nephrurus sphyrurus	01010001A000AA1B111000B110B0AAAA1000A00010B1000A10AA0A090110099900ABAB1A1A000000191101110B0A0000
Nephrurus stellatus	01010001A000AA1B111000B111BAAAA10100A110B02001A10AA1100A0110199901ABAB1A0B000000191101111B0A0000
Nephrurus vertebralis	01010001A000AA0B1110000B011BAAAA10100A110B12001A10AA1100A0110199901ABAB1A0B000000191101111B0A0000
Nephrurus wheeleri	91010001A000AA0B111000B9991BAAAA10100A110B101001A10AA1000A0110199901ABAB1A0B000000191101111B0A0000
Phyllurus caudiannulatus	11100011A010AA1B1110000B111BAAAA00010A011A011A011A019A0001A00AAA090011000B0A0000000191101900B0A0000
Phyllurus cornutus	11101011A010AA1B1110000B011BAABA0091A011A011A0110A011A019A0001A00AAA090011000B0A00000191101900B0A0000
Phyllurus platurus	11100011A010AA1B1110000B011BAABA00010A011A010111A0011A0001A00AAA090011000B0A0000000191101900B0A0000
Phyllurus salebrosus	11101011A010AA1B1110000B011BAABA0009A011A011A011A0119A0001A00AAA1B0A000000A191100B0A0000
Rhacodactylus auriculatus	00011100A0101BB1A0000001A00009AABB00000A000B00B0010A00AAA090A1010100B0A0000A0B0101
Rhacodactylus australis	10001000A000BB0A00000011A00009AABB00000B000A00000B00B00A0A0BB0A000001191108BA090A001000B0A0000A1A0101
Rhacodactylus cavaticus	09999999999999990999999990A9999999999999091910A0BAA090A00010011910A09AA090001A0109
Rhacodactylus chahoua	00011000A000BB0A0000001A00009BAAB00000A000A00000B00B0010A00BAAA090A001011110A0A0000A190101
Rhacodactylus ciliatus	00011000A101BB0A0000001A00009BAAB00000A000A00000B00B0010A00BAAA090A1011100A0A0000A1B0109
Rhacodactylus leachianus	10011100A000BB1A0000001A10009ABA00000A000A00000B00B0010A00BAAA090A00101110A0A0000A1B1101
Rhacodactylus lindneri	00011000A000BB0A0000001A00009AAAA00000B00B0010A00BAAA090A0010000B0A0000A1A0101
Rhacodactylus sarasinorum	10011000A000BB0A0000001A00009AABB00000A000A00000B00B0010A00BAAA090A10100A0A0000A190901
Rhacodactylus trachyrhynchus	10011000A000AA9B0A0000001A00009AABB00000B000A00000B00B0010A00BAAA090A10100B0A0000A1B0111

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KONRAD FIEDLER

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Systematic, evolutionary, and ecological implications of myrmecophily within the Lycaenidae (Insecta: Lepidoptera: Papilionoidea)

by

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CONTENTS

ABSTRACT

1.) A quantitative study of the behavioural interactions of 7 European Lycaenidae and 1 Riodinidae species with 2 ant species revealed significant differences between myrmecophilous and myrmecoxenous caterpillars. A functional dorsal nectary organ is decisive for stable ant-associations. Further aspects of the function of the myrmecophilous organs, and the application of the proposed experimental method to comparative surveys are discussed.

2.) The presence of myrmecophilous organs in lycaenid larvae and the shape of their interactions with ants are intimately correlated with the higher classification of the family. The hypothesis of ancestral myrmecophily is rejected, the decisive dorsal nectary organ being an important synapomorphy of the most advanced subfamily Lycaeninae. The characteristic states of myrmecophily are discussed for all higher lycaenid taxa.

3.) Only trophobiotic ant taxa are involved in non-aggressive interactions with lycaenids. Obligatory myrmecophily is mainly confined to ecologically dominant ants that form large, long-lived colonies, and most of such relationships occur in only a limited number of lycaenid lineages, suggesting the occurrence of phyletic preadaptations for obligatory myrmecophily in these particular taxa.

4.) Lycaenidae caterpillars mainly feed on plants of the subclass Rosidae with a distinct predilection of Fabales and Santalales. The hostplant patterns of the higher lycaenid taxa are described. There is little overlap between hostplant patterns of the Lycaenidae and other butterfly families. In contradiction to a recent hypothesis, no close correlation between myrmecophily and the predilection of Fabales or Santalales was found, with roughly 50 % of the myrmecophiles utilizing different foodplants. Neither obligate nor facultative myrmecophiles consistently have a wider hostplant range than myrmecoxenous species, indicating that myrmecophily has only exceptionally influenced the hostplant relationships of lycaenid caterpillars.

5.) The geographic distribution of myrmecophily is intimately correlated with the distribution of the higher lycaenid taxa. Gross patterns of lycaenid distribution point towards an important role of plate tectonics in the separation of the major lineages. The lycaenid faunas of 8 regions are systematically described, and the proportions of ant-associated species are estimated. A clear north-south disparity in the proportion or degree of myrmecophily is not discernible.

6.) Some hypotheses concerning the evolution of myrmecophily in relation to the phylogeny of the Lycaenidae are proposed. Ant-associations have evolved in parallel in 2 lineages (Miletinae and Lycaeninae). In particular, specializations in, and reductions of, myrmecophily are discussed.

7.) An Appendix summarizes data on hostplants and myrmecophily of more than 1000 Lycaenidae species.

INTRODUCTION

Lycaenid myrmecophily: the general framework

The insect order Lepidoptera comprises 150,000—200,000 described species of which only 13,000—15,000 constitute the well-known butterflies (Papilionoidea; Shields 1989a). The Papilionoidea are divided into five probably monophyletic units that usually are given family rank (Papilionidae, Pieridae, Lycaenidae, Riodinidae, and Nymphalidae). Although often treated as a subfamily of the Lycaenidae, recent research on the mainly neotropical Riodinidae supports the distinction of these 2 taxa (Harvey 1987).

In any case the Nymphalidae and Lycaenidae *s. str.* together contain more than 75 % of the whole species diversity of butterflies and this poses the intriguing question as to what selective conditions have led to this predominance. Starting from their common *Bauplan*, the c. 6,500 nymphalid species show a huge diversification in both morphology and biology. This results in a considerable number of monophyletic subunits that can be characterized by their distinctive morphology and/or host-plant preferences (Ackery 1988).

The phylogenetic relationships among the nymphalid groups are not yet resolved and several of these subunits are still treated as distinct families on a merely typological basis. Generally, the evolutionary strategy of the Nymphalidae can be viewed as adaptive radiation into distinct lineages.

In contrast, the Lycaenidae with about 4,400 species (Bridges 1988), are decidedly more homogeneous. The currently recognized 4 subfamilies (Scott & Wright 1990, this study) have rarely been treated as distinct families (see Stempffer 1967 and Eliot 1973 for historical reviews), and the vast majority of species belongs to a single subfamily, the Lycaeninae.

Thus, the adaptive radiation of the Lycaenidae is largely a phenomenon inside one lineage. Several authors (e.g. Malicky 1969b, Atsatt 1981a, Pierce 1984) have suggested that one factor could have played an important role in this evolutionary process: the interactions of numerous Lycaenidae with ants, termed myrmecophily.

Ants are the leading evertebrate predators of arthropods (Hölldobler & Wilson 1990), and they exert a significant selective pressure on lepidopterous larvae in particular (e.g. Tilman 1978, Laine & Niemelä 1980, Warrington & Whittaker 1985, Jones 1987, Whalen & Mackay 1988, Gösswald 1989, Ito & Higashi 1991).

A number of defensive strategies of caterpillars apply, at least in part, to the avoidance of fatal ant attacks. Among these are defensive regurgitations (Common & Bellas 1977, Eisner et al. 1980, Leather & Brotherton 1987, Peterson et al. 1987) or defensive secretions (e.g. Eisner et al. 1970, 1972, Honda 1983a, b), a dense coating with hairs (Ayre & Hitchon 1968, Weseloh 1989), or the construction of protective silk-webs (Ito & Higashi 1991).

A totally different strategy is to coexist with ants in a non-aggressive way. Such coexistence can be seen as myrmecophily in the widest sense, and DeVries (1991) has recently emphasized that ignorance, i.e. indifferent coexistence of predatory ants with caterpillars, is an important step in the evolution of truly myrmecophilous interactions (see also Atsatt 1981a).

Caterpillars are usually rather slowly moving insects with a soft cuticle and are thus almost a prototype of ant prey. Nevertheless, myrmecophily is amazingly widespread within the Lepidoptera, but unfortunately most published reports refer to rather anecdotal observations, and only very few cases of Lepidopteran myrmecophily, outside the Lycaenidae and Riodinidae, are yet sufficiently well understood.

The larvae of several species in various moth families (Tineidae, Psychidae, Cyclotornidae, Batrachedridae, Pyralidae, Noctuidae, Arctiidae; see Hinton 1951, Hölldobler & Wilson 1990 and Tab.1 for further references) are known to live among ants or inside ant nests. There are commensales or refuse-feeders (*Myrmecozela, Atticonviva* [Tineidae], *Pachypodistes* [Pyralidae]), scavengers (e.g. *Iphierga* and *Ardiosteres* [Psychidae], *Epizeuxis* [Noctuidae]), or predators of ant-brood (*Hypophryctoides* [Tineidae], *Batrachedra* [Batrachedridae], *Cyclotorna* [Cyclotornidae]; *Wurthia* and *Niphopyralis* [Pyralidae]). In *Cyclotorna* the relationship to its host-ant genus *Iridomyrmex* is even more intimate: second instar larvae are actively adopted by these ants that also imbibe the larval excretions. Larvae of the Palaearctic noctuid *Conistra (Dasycampa) rubiginea* often enter nests of the ant *Lasius fuliginosus* for pupation, but the details of this relationship remain unknown. Caterpillars of the Oriental tortricid genus *Semutophila* produce anal exsudates containing carbohydrates, and these excretions induce truly trophobiotic associations with ants.

Non-aggressive ant-caterpillar interactions sometimes occur when ants visit lepidopterous larvae while feeding and imbibe the sap flow caused by the caterpillars' feeding activities. Such associations have been reported from several *Ethmia* species (Oecophoridae), the noctuid genus *Othreis*, the pierid genus *Eurema*, and from some Lycaenidae (*Curetis regula*: DeVries 1984; *Lycaena dispar*: Elfferich, pers. comm.). Caterpillars of the Oriental noctuid genus *Homodes* live among weaver ants (*Oecophylla smaragdina*), apparently without being attacked and mimicking the host ants with the help of peculiar epidermal appendages (Kalshoven 1961, Common 1990, Fiedler, pers. observations). Ford (1945) reported that some Pieridae caterpillars are visited by ants that lick up secretions from glandular hairs. However, these secretions are thought to be primarily defensive, at least in the Palaearctic *Gonepteryx rhamni* (Wasserthal, pers. comm.).

A very unusual observation was reported by Ebner (1905): Caterpillars of the saturniid moth *Saturnia pyri* were visited by small red ants (possibly *Myrmica* sp.?) that licked up the defensive secretions from the caterpillars' scoli. A recent investigation of the related *Saturnia (Eudia) pavonia* revealed that these secretions contain proteins, polypeptides and several aromatic compounds (Deml & Dettner 1990). A summary of these caterpillar-ant associations outside the Riodinidae and Lycaenidae is given in Tab.1.

Tab.1: Ant-associations of Lepidoptera caterpillars other than Riodinidae and Lycaenidae.

Family/ Species	Interaction with ants	References
Tineidae:		
Myrmecozela spp.	feeding on nest material and as scavengers in *Formica* nests	Hinton 1951, Emmet 1979
Hypophryctoides dolichoderella	predator of ant pupae in nests of *Hypoclinea* and *Anoplolepis*	Roepke 1925
Atticonviva spp.	feeding on plant material in *Atta* and *Acromyrmex* nests	Hölldobler & Wilson 1990
Psychidae:		
Iphierga spp.	scavengers in nests of	Dodd 1912,
Ardiosteres spp.	*Iridomyrmex*	Common 1990
Batrachedridae:		
Batrachedra myrmecophila	predator of ant brood in nests of *Polyrhachis dives*	Hinton 1951
Oecophoridae:		
Ethmia spp.	ants (*Lasius, Formica, Myrmica*) visit feeding places to imbibe sapflow	Thomann 1908
Cyclotornidae:		
Cyclotorna spp.	first instars ectoparasitic on Jassidae, Psyllidae, Cicadellidae, later instars predatory in *Iridomyrmex* nests	Dodd 1912, Common 1990
Saturniidae:		
Saturnia pyri	red ants (*Myrmica* sp.?) lick up defensive secretions from scoli	Ebner 1905
Lasiocampidae:		
Macrothylacia rubi	3rd instar larva found under stone with large *Lasius* nest, ignored	Fiedler, own observation
Tortricidae:		
Semutophila saccharopa	ants (7 genera) feed on anal exsudates (trophobiosis)	Maschwitz et al. 1986
Pyralidae:		
Pachypodistes goeldii	feeds on nest carton of *Hypoclinea gibbosoanalis*	Hagmann 1907
Wurthia spp.	predators of ant brood in *Oecophylla* and *Polyrhachis* nests	Roepke 1916, Kemner 1925

Family/ Species	Interaction with ants	References
Niphopyralis chionensis	scavenger in ant nests	Common 1990
Stenachroia *myrmecophila*	found in *Crematogaster* galleries	Hölldobler & Wilson 1990
Arctiidae:		
Crambidia casta	larvae feed on lichen in and near *Formica* nests, pupate in the nests	Ayre 1958
Noctuidae:		
Epizeuxis americalis	scavenger in *Formica* nests	Smith 1941
Conistra rubiginea	pupates in nests of *Lasius fuliginosus*	Hinton 1951, Maschwitz, pers. comm.
Homodes spp.	live as mimics among *Oecophylla* ants, relationship unknown	Kalshoven 1961, Common 1990
Othreis fullonia	ants (*Dolichoderus*) visit feeding places, imbibe sapflow	Leefmans 1933
Eublemma albifasciata	larvae receive ant regurgitations and feed on eggs in *Oecophylla* nests	Dejean 1991
Pieridae:		
Catopsilia florella	ants visit feeding places and imbibe sapflow	Leefmans 1933
Pieris spp., *Anthocharis cardamines*, *Leptidea sinapis*	ants lick up secretions from glandular hairs	Ford 1945, Hinton 1951

A number of further cases of caterpillar myrmecophily will undoubtedly be detected in the course of future research, especially in families such as Tineidae, Pyralidae and Noctuidae, and in tropical regions. However, most of these cases of ant-associations refer to single exceptions in species-rich families where the majority of larvae do never associate with ants.

In addition, no peculiar myrmecophilous organs (e.g. glands) are hitherto known from them. Instead, these caterpillars largely rely, as far as is known today, upon protective silk-webs (*Myrmecozela, Semutophila*), cases built from plant or nest material (Psychidae, Pyralidae) etc. Chemical camouflage via acquired host odour may well be involved as in one myrmecophilous scarabaeid beetle (VanderMeer & Wojcik 1982). In addition, chemical mimicry with the help of cuticular hydrocarbons as exhibited by myrmecophilous syrphid larvae of the genus *Microdon* may also occur (Howard et al. 1990).

In the butterfly families Riodinidae and Lycaenidae, however, numerous species associate with ants. Harvey (1987) estimated the number of myrmecophilous Riodinidae to about 250 species, and in the Lycaenidae more than 3,000 species may be associated with ants. The ant-associated larvae of both families possess a number of highly specialized myrmecophilous organs, and these organs as well as some further adaptations are the basis for their myrmecophilous interactions which by far exceed other cases of lepidopteran myrmecophily in terms of both diversity and complexity.

In this monograph I shall only discuss the myrmecophily of the Lycaenidae s. str. with main focus on caterpillar-ant interactions. The pupae of many Lycaenidae as well as the adults of some species, too, associate with ants, and both phenomena will be considered where appropriate.

The myrmecophily of lycaenid pupae has been discussed in detail by Fiedler (1988a). Bourquin (1953), Ross (1964a, 1966), Callaghan (1977, 1982, 1986a, b, 1989), Schremmer (1978), Horvitz & Schemske (1984), Horvitz et al. (1987), Harvey (1987), and DeVries (1988, 1990a, b, 1991) gave important accounts of the larval biology and myrmecophilous relationships of the family Riodinidae.

Non-aggressive associations of caterpillars with ants attracted the attention of the early naturalists in the second half of the 18th century. By the middle of the 19th century, several European lycaenids were already known to have myrmecophilous caterpillars, and in 1867 Guenée first described the dorsal nectary organ. In the following decades a growing body of evidence was built up concerning life-histories of lycaenids including numerous tropical species.

However, most of these reports were purely descriptive or even anecdotal, and this continues to a considerable degree until today. The first detailed morphological and histological investigations of the myrmecophilous organs were carried out by Newcomer (1912) and Ehrhardt (1914), and by the middle of this century the scattered information had been compiled and thoroughly reviewed twice (Warnecke 1932/33, Hinton 1951).

It was Malicky who laid the basis for our current knowledge of lycaenid-ant interactions in his outstanding extensive compilatory and experimental studies (1969a, b, 1970a, b). During the last decade the myrmecophilous relationships of the Lycaenidae have again received enhanced attention. Pierce and her coworkers focused on the behavioural ecology of, and selective forces acting in, caterpillar-ant interactions (Pierce & Mead 1981, Pierce 1983, 1989, Pierce & Elgar 1985, Pierce & Eastseal 1986, Pierce & Young 1986, Pierce et al. 1987 & 1990, Smiley et al. 1988, Elgar, Pierce 1988).

Furthermore, Pierce (1984, 1985, 1987) and Pierce & Elgar (1985) proposed some hypotheses concerning the evolution and biogeography of lycaenid myrmecophily that were readily taken up in general textbooks on behavioural ecology and evolution.

Henning (1983a, b) studied the chemical communication between caterpillars and ants, and Fiedler & Maschwitz (1988a, b, 1989a, b) analysed certain behavioural interactions. Cottrell (1984) gave a detailed modern review, and the description of life histories was

continued by a number of authors. As a basis for the main topics of this study, I give a comprehensive summary of the current state of the knowledge about myrmecophily of the Lycaenidae in the following two chapters.

Morphology and function of the myrmecophilous organs of lycaenid caterpillars

The adaptations of lycaenid caterpillars towards myrmecophily can roughly be divided into two categories: "passive" protective characters and "active" exocrine glands. The most important passive preadaptation is the unusually thick and tough cuticle of most lycaenid larvae. As has been demonstrated by Malicky (1969b), the cuticle of lycaenid caterpillars is 5—20 times thicker than that of other lepidopteran caterpillars of comparable size.

In addition, most lycaenid larvae have a peculiar *gestalt* that has often been compared with that of woodlice ("onisciform"): their dorsum is weakly rounded, while the flat venter adheres tightly to the substrate.

Furthermore, most lycaenid larvae can retract their head completely under their prothoracic shield. Thus, the most vulnerable organs (nervous system) are well protected against possible ant-attacks, and the shape of their body together with the toughness of their cuticle allow most larvae to withstand occasional hostile reactions of the ants (Malicky 1969b, 1970a, b; but see Samson & O'Brien 1981).

Other preadaptations are found in the larval behaviour. Usually lycaenid caterpillars move very slowly, and they normally lack the thrashing reflex (Malicky 1969b) that is exhibited by many lepidopterous caterpillars when disturbed (Cornell et al. 1987). Since fast movements and thrashing often cause ants to attack, these behavioural peculiarities are important prerequisites for more advanced myrmecophilous interactions.

By far most important for the maintenance of ant-associations are the myrmecophilous organs of lycaenid caterpillars. Three types of such organs are sufficiently well known, although information on the chemical composition of their secretions is still extremely fragmentary.

The first type are the **pore cupola organs (PCOs**; the terminology of ant organs follows Cottrell 1984 throughout). The PCOs are small glandular structures that are derived from hairs, with the hair shaft transformed into a sieve-plate with numerous minute pores of 0.1—0.2 μm diameter. PCOs occur in both lycaenid larvae and pupae and have been observed in all but one of the species investigated so far (e.g. Malicky 1969b, Ballmer & Pratt 1988).

However, morphology and distribution of the PCOs differ markedly between the subgroups of the Lycaenidae, Miletinae and Curetinae bearing particularly aberrant types (DeVries et al. 1986, Kitching 1987, own unpublished observations). PCOs are present from the first instar on, but generally their number increases with every moult, mature larvae possessing most of them (Malicky 1969b, own observations).

Furthermore, the majority of lycaenid caterpillars have concentrations of PCOs around the spiracles and (if present) around the dorsal nectary organ (see below). Highly myrmecophilous caterpillars seem to bear more PCOs equipped with greater pores (Fiedler, unpublished), but these observations need confirmation based on a larger sample of species.

Sometimes the pores are so minute that they can hardly be detected on SEM photographs. Malicky (1969b, 1970a), based on classical light microscopy, termed such organs lenticles, but since even lenticles of non-myrmecophilous hesperiid larvae have turned out to possess pores when studied with sufficient resolution (Franzl et al. 1984), this distinction is of limited value.

Only one lycaenid species definitely lacks PCOs: *Liphyra brassolis* larvae live as brood predators inside the nests of the extremely aggressive weaver ant, *Oecophylla smaragdina*, where they are protected against attacks by an unusually thickened, carapax-like cuticle (Cottrell 1987, Ballmer & Pratt 1988). Obviously this species has lost the PCOs in favour of an alternative defensive strategy.

The presence of PCOs in the rather large Palaeotropical subfamily Poritiinae requires confirmation using electron microscopy, but the illustrations of Clark & Dickson (1971) indicate that lenticle-like structures are present. All other lycaenid and riodinid larvae examined so far possess PCOs at least around the spiracles.

In 1951, Hinton suspected the PCOs to be the source of substances attractive to ants. This has then been established in considerable detail by Malicky (1969b, 1970a) who demonstrated that the PCOs cause intensive antennation behaviour in ants attending lycaenid larvae.

He also distinguished between two types of antennal reaction of the ants towards lycaenid caterpillars: "groping" (stroking with low frequency and intensity), and "palpation" (intensive and high-frequent antennal stimulation). The latter was typically observed at dense clusters of PCOs or at the DNO, while the former is an ubiquitous exploratory behaviour of many ants to assure the nature of newly discovered objects.

Malicky further proved the glandular nature of the PCOs for a number of species and concluded, based on extensive histological and behavioural observations, that the PCOs play the most important role in mediating lycaenid myrmecophily. No myrmecophilous larvae had at that time ever been found without PCOs, while a number of species with no further myrmecophilous organs present apparently released the same behaviour in attendant ants as those lycaenid larvae with more complex myrmecophilous organs.

Malicky's view has subsequently been adopted by a number of authors (e.g. Henning 1983a, b, Kitching & Luke 1985), but was recently questioned by Fiedler & Maschwitz (1989a, 1990; see below).

Although the important role of the PCOs in the interactions between lycaenid larvae and ants is now well established, the chemical composition of their secretions remains practically unknown. Pierce (1983) found amino acids in extracts obtained by washing pupae of the North American polyommatine species *Glaucopsyche lygdamus*, and the

amounts of amino acids detected in the extracts were highly correlated with the attractiveness of the pupae to ants. But she could not completely rule out the possibility that these amino acids originated from other pupal structures (e.g. dendritic hairs, see below). Furthermore, since pupae of *G. lygdamus* sometimes have a functional dorsal nectary organ (Downey 1965), the presence of amino acids in the PCO secretions needs confirmation.

It is clear from behavioural observations that the chemical signals released by the PCOs must be rather general in facultatively myrmecophilous lycaenids, because in numerous cases ants from different genera or even subfamilies react to the same lycaenid immatures in a similar way (Malicky 1969b, Fiedler, unpublished). Thus, mimics of ant brood pheromones (as supposed by Malicky 1969b) are unlikely to be involved in these cases, while amino acids, to which ants are generally attracted as food, are indeed likely candidates.

In obligatorily myrmecophilous lycaenids that are associated with specific host ant genera or species, only these specific ants adequately respond to the secretions of lycaenid larvae (Pierce 1989).

At least in the Palaearctic genus *Maculinea*, whose larvae live as parasites in *Myrmica* ant nests, brood pheromone mimics are probably used by the larvae (Elmes et al. 1991a, b), and it is well possible that these substances originate from the extremely numerous PCOs of *Maculinea* caterpillars (Fiedler, unpublished). The chemical nature of these adoption substances is unknown, but cuticular hydrocarbons are possibly involved (see Howard et al. 1990 for a parallel case of syrphid myrmecophily; also Brian 1975).

In the Australian genus *Jalmenus*, different concentration profiles of amino acids in the secretions of the dorsal nectary organ are responsible for the recognition and acceptance of the larvae by their appropriate host ants (Pierce 1989), and this may apply to their PCO secretions as well. Several ants are known to respond differentially to the presence and concentrations of various amino acids (Lanza 1988, Lanza & Krauss 1984).

However, not all lycaenid PCOs are attractive to ants. For example, caterpillars of *Callophrys rubi*, although possessing PCOs, were never palpated in experiments with ant species of two subfamilies (Fiedler 1990d). Similarly the PCOs of some riodinid larvae (including myrmecophilous species) are unattractive to ants (DeVries 1988, Harvey 1989), and Ballmer & Pratt (in press) observed very different reactions of *Formica pilicornis* ants to a number of Californian riodinid and lycaenid caterpillars, ranging from permanent attendance to severe attacks (see also Malicky 1970b).

Since all these species tested have PCOs, differences in the function of these organs apparently do exist. Hence, although the important role of the PCOs is clearly documented in many lycaenids, the chemical composition of their secretions and their related biological functions provide a challenge for further investigation.

The second type of myrmecophilous organs is the **dorsal nectary organ (DNO)**, an epidermal gland located on the dorsum of the seventh abdominal segment. Usually the orifice of the DNO is surrounded by a cluster of PCOs and very often by a field of

specialized setae (club-shaped setae, dendritic hairs etc.: Clark & Dickson 1956, 1971, Kitching & Luke 1985, Fiedler 1988b).

The DNO secretes droplets of a clear fluid when stimulated by ants via antennation. Normally attendant ants vigorously palpate the vicinity of the DNO and eagerly imbibe each droplet (Malicky 1969b). The hairs surrounding the DNO are supposed to be sensory, but this requires experimental confirmation.

Malicky (1969b, 1970a) provided evidence that the DNO itself could be derived from hairs, while Kitching & Luke (1985) presumed that the DNO may have evolved from one of the numerous epidermal pores commonly found on lycaenid caterpillars.

In contrast to the PCOs, a functional DNO is usually not present in the pupal stage, although many pupae still bear a scar of the DNO. The only exception was reported from *Glaucopsyche lygdamus*, where Downey (1965) observed a functional DNO in some pupae that all died later.

The ontogeny of the DNO and the mechanism of its function were described in detail by Malicky (1969b). The DNO is normally present and functional from the third larval instar on. There is, however, some variation. In some species the DNO's appearance is delayed until the fourth stage, in very few species it already starts working in the second instar (Clark & Dickson 1956, 1971).

The chemical composition of the DNO secretions is known from only a couple of species. In the secretions of *Polyommatus hispanus* and *P. icarus*, several carbohydrates (total concentrations 10—15 %), but only traces of amino acids were found (Maschwitz et al. 1975). Pierce (1983, 1989) reported variable amounts of carbohydrates and high concentrations of amino acids from *Glaucopsyche lygdamus* and 3 Australian *Jalmenus* species, while in *J. daemeli* the amino acids are apparently replaced by a characteristic oligopeptide. In the riodinid *Thisbe irenea* the secretions from the analogous tentacle nectary organs likewise contain high concentrations of amino acids (DeVries & Baker 1989).

These limited data and the fact that usually attendant ants imbibe the DNO secretions immediately indicate that these secretions provide a valueable food source for ants. Evidently the nutritive compounds are derived from the caterpillars' food, and recent experimental work has shown that the quality of larval food may affect the ability of the larvae to produce their myrmecophilous secretions (Fiedler 1990c, Baylis & Pierce 1991). However, any speculations about systematic or geographical traits (e.g. Pierce 1987) in the composition of the DNO secretions must await further data from a broader spectrum of species.

The DNO is by no means as ubiquitous in the larvae of the Lycaenidae, as are the PCOs. In fact, it is known only from the subfamily Lycaeninae, and even there it is secondarily missing in a number of species or genera. Accordingly, Kitching & Luke (1985) suggested to term all those species without a DNO **"myrmecoxenous"**, a distinction that turned out to be of considerable value for the discussion of the evolutionary and systematic implications of lycaenid myrmecophily (see below).

Throughout this study only species with a functional DNO are called **myrmecophilous** from a morphological point of view. Interestingly, and in contrast to an often repeated belief (e.g. Malicky 1969b), ant-associations of lycaenid larvae without a functional DNO are rare and mostly occur under special circumstances (e.g. carnivorous species). Myrmecophilous Riodinidae possess a pair of tentacle nectary organs that are functionally comparable, but phylogenetically only analogous to the DNO (Cottrell 1984, DeVries 1988).

A third type of myrmecophilous organs are the eversible **tentacle organs (TOs),** a pair of epidermal tubes located on the dorsum of the eighth abdominal segment of many lycaenid caterpillars. The TOs are everted when the larvae are stimulated by ants or, in some species, when the caterpillars crawl about or are disturbed.

When the everted TOs are touched, they are withdrawn immediately. Normally the TOs of each side of the body are able to act independently from one another, and often the sequence of eversion and retraction of the TOs is repeated several times, resulting in a conspicuous tentacle performance. On the top of each tentacle there are numerous setae, mostly of a dendritic type. The TOs are everted by means of a locally increased hemolymph pressure mediated by the abdominal dorsoventral musculature of the larvae, and they are withdrawn by a peculiar retractor muscle (Malicky 1969b).

Morphologically there are 2 main types of TOs: the rather small "beacon" type that is widely distributed among the subfamily Lycaeninae, and the larger "whip" type that only occurs in the Aphnaeini (Clark & Dickson 1956, 1971). The TOs of the Curetinae (DeVries et al. 1986, Fiedler & Maschwitz, unpublished) are somewhat similar to the Aphnaeini TOs in size and structure.

The function of the TOs has been the subject of controversy over several decades. Based on behavioural observations several early authors (e.g. Thomann 1901) supposed the TOs to be scent organs influencing the ants' behaviour. Ehrhardt (1914) stated that the dendritic hairs on their top are glandular, based on his observation that these hairs bear very large pyriform cell bodies.

Malicky (1969b, 1970a), however, rejected these findings. He was neither able to detect any glandular structures within the TOs, nor any reaction of the ants towards the eversion of these organs (but see Malicky 1961), and he concluded that the TOs of lycaenid caterpillars were nothing more than rudiments of formerly important organs.

However, a number of authors have reported that attendant ants do respond to the eversion of the TOs with alertness or even alarm behaviour (Elfferich 1963b, 1965, Downey & Allyn 1979, Fiedler & Maschwitz 1988b, 1989b, Munguira & Martin 1988, 1989b, Schurian 1989a, Jutzeler 1989a, Ballmer & Pratt in press). This reaction is usually only observed in a radius of a few mm around the TOs.

Furthermore, not all ant species react to the TOs of a given lycaenid species. With the only exception of *Aricia morronensis* (where the dolichoderine ant genus *Tapinoma* showed the characteristic "excited runs": Munguira & Martin 1988), the ants hitherto observed to respond to the TOs all belong to the subfamily Formicinae.

This group-specificity of the reaction observed, and the short active range of the releasing signal, led to the assumption that the TOs produce volatile secretions (possibly mimics of ant alarm-pheromones) causing the alertness of attendant ants. Alarm-pheromones of ants generally are highly volatile, have a short active range, and often one major component occurs in larger systematic groups of the Formicidae (Hölldobler & Wilson 1990).

Chemical support for this pheromone-mimic hypothesis comes from the study of Henning (1983b) who demonstrated that the TOs of the South African Aphnaeini species *Aloeides dentatis* and the alarm-pheromone of its obligate and specific host ant *Acantholepis capensis* yield very similar gas-chromatographic profiles. In 1977, Claassens & Dickson had already demonstrated that caterpillars of the closely related *Aloeides thyra* alert the same host ant species with their TOs when travelling between their feeding places and the ant nests, wherein the caterpillars rest.

Thus, although the ultrastructure of the TOs and the detailed chemical composition of their presumed volatile secretions remain to be examined more closely, there can be no doubt that at least in a number of lycaenid species the TOs are able to activate specific attendant ants.

TOs are present only in the larvae of the subfamilies Curetinae and Lycaeninae (regarding the genus *Aslauga* [Miletinae] see below), but they are missing in even more species and genera than the DNO. Generally, larvae with TOs also possess a DNO, and there are only very few well-documented examples where the larvae only have the TOs (*Curetis*, some *Aloides* spp.). The reverse situation (bearing a DNO, but without TOs), in contrast, is rather common.

In the caterpillars of Theclini, Eumaeini, and Polyommatini the beacon type TOs usually, but not always appear together with the DNO in the third instar. In some species, their appearance is delayed until the fourth stage, in others they develop already in the second (Clark & Dickson 1956).

In Aphnaeini larvae, in contrast, the whip type TOs are present throughout the whole larval period. In this tribe, the DNO develops in the second or third instar. Some species apparently have no DNO at all (*Phasis*), whereas in others it disappears in the ultimate instar (*Aloeides dentatis*?; Clark & Dickson 1956, 1971).

Besides the three main types of myrmecophilous organs (PCOs, DNO, TOs) further larval and pupal characters may be related with myrmecophily. Ballmer & Pratt (1988 and in press) suggest that dendritic setae secrete ant-attractive substances.

Support for this hypothesis comes from the observation that concentrations of dendritic hairs on lycaenid larvae or pupae receive considerably enhanced attention by ants (e.g. spiracles of the prothoracic and sixth abdominal segment of *Polyommatus* or *Lycaena* pupae: Malicky 1969b, Fiedler 1987a). The only four North American *Lycaena* species, that are regularly ant-attended in the field, possess dendritic setae already as larvae. In other *Lycaena* species such setae are confined to the pupae, if they are present at all (Wright 1983, Fiedler 1988b and unpublished, Ballmer & Pratt in press).

Morphological surveys of numerous lycaenid immatures revealed a large diversity of further specialized setae and epidermal pores whose function is still unknown (e.g. Clark & Dickson 1971, Downey & Allyn 1978, 1979, Wright 1983, Kitching 1983, 1987, Kitching & Luke 1985, DeVries et al. 1986, Baylis & Kitching 1988, Fiedler 1988b, 1990d and unpublished results). Some of these structures might play a role in the interactions with ants, as well.

Recently, DeVries (1990a) detected the production of substrate-borne vibrations in myrmecophilous Riodinidae and Lycaenidae larvae. Riodinids "stridulate" with the help of peculiar organs, the "vibratory papillae". In at least one species, *Thisbe irenea*, such vibrational signals enhance the ant-associations of the larvae (DeVries 1988, 1991).

Substrate- as well as air-borne vibrational signals were also found in larvae of several lycaenids (e.g. European *Maculinea, Polyommatus, Cupido* and *Lycaena* species: DeVries 1990a, Schurian, Fiedler & Tautz, unpublished). The mechanism of sound production by lycaenid caterpillars is still unknown. A connection of larval sound production with myrmecophily needs to be proven, but must be taken into account.

The pupae of many lycaenids and riodinids are likewise able to stridulate with a specialized organ located between two abdominal tergites (Hoegh-Guldberg 1972, Downey & Allyn 1973, 1978, Elfferich 1988). This pupal stridulation, however, is currently interpreted mainly as a defensive device (Hoegh-Guldberg 1972, Downey & Allyn 1978).

Adults of a number of lycaenid species also live in associations with ants, particularly in the subfamily Miletinae. Morphological or biochemical adaptations are suspected to occur, but nothing certain is known. Imaginals of several non-related species that pupate in ant nests bear a dense covering of loose hairy scales at eclosion, which prevent ant-attacks while leaving the host nest (Cottrell 1984, 1987).

Communication between lycaenid caterpillars and ants

Lycaenid caterpillars clearly influence or manipulate the behaviour of ants they encounter. First, instead of being attacked and killed as prey, they suppress ant-aggressiveness and are thus normally vigorously palpated or at least ignored by the ants. Ignorance (DeVries 1991) or appeasement (Maschwitz et al. 1985b) are obviously the premise of more complex interactions.

Any caterpillar that fails to appease or deter the ants encountered has a low chance of survival. The chemical basis of appeasement or ignorance is still weakly understood. It has repeatedly been assumed that the PCOs' secretions are responsible for the suppression of ant-aggressiveness (Maschwitz et al. 1985b, Fiedler & Maschwitz 1989a etc.), and the general presence of the PCOs in lycaenid immatures, in concert with the widespread attractiveness of their secretions to ants, strongly support this view.

If the secretions of the PCOs are really basically amino acids (see above), then the "appeasement" of ants is mediated through nutritive components instead of pheromone

mimics. This seems to apply to the great number of facultatively myrmecophilous lycaenids that unspecifically associate with a wide array of ant species.

Furthermore, as has been discussed by Pierce (1989), amino acids may secondarily well play important roles as communicative substances in ants, and she presented evidence that differential responses of ants towards amino acids (see Lanza & Krauss 1984, Lanza 1988) are used in the specific communication of the Australian lycaenid genus *Jalmenus* with its different specific host ants.

In some obligatorily myrmecophilous lycaenids with specific host ants, the caterpillars are able to release brood-carrying behaviour in their appropriate host ants. In these cases mimics of the recognition substances of ant workers or ant brood are suspected.

In ants, such recognition substances are usually cuticular hydrocarbons (Hölldobler & Wilson 1990), and several myrmecophilous insects indeed possess hydrocarbon profiles similar to that of their hosts. These substances may be passively acquired (Scarabaeidae: VanderMeer & Woijcik 1982) or actively biosynthesized (Syrphidae: Howard et al. 1990).

For lycaenid larvae no exact chemical data exist, but Henning (1983b) demonstrated that epidermal extracts of *Lepidochrysops ignota* caterpillars induced carrying and brood-caring behaviour in the specific host ant, *Camponotus niveosetosus*. The rapid adoption of larvae of *Maculinea alcon* and *M. rebeli* (Elmes et al. 1991a, b), *M. nausithous* (Fiedler 1990b), or *Anthene emolus* (Fiedler & Maschwitz 1989b) suggests that these larvae, as well, actively produce the allomones required, whether through the PCOs or elsewhere in the cuticle.

Furthermore, myrmecophilous lycaenid larvae are able to induce food recruitment in their attendant ants by offering their DNO secretions (Fiedler & Maschwitz 1989a). The alerting of attendant ants with the help of the TOs and the possible vibrational communication of lycaenid larvae have already been mentioned.

Summarizing the available evidence, trophic as well as communicative substances certainly govern the interactions of lycaenid caterpillars with ants, with mechanical stimuli as a potential communicative supplement. The ants usually react with antennal stroking or intensive palpation to these signals, and they regularly harvest the caterpillars' secretions.

The communication mechanisms of adult lycaenids remain obscure. Adult Miletinae and Poritiinae often visit ant-homopteran associations to imbibe honeydew without being attacked. The ants regularly touch the butterflies or even climb their legs and wings (Maschwitz et al. 1985a, 1988).

One African Poritiinae species, *Teratoneura isabellae*, apparently deters ants using a volatile chemical (Farquharson 1922). In a number of obligatorily ant-associated lycaenids, the females oviposit amongst their host-ants with no aggressiveness being observed (Atsatt 1981b, Henning 1983a, Cottrell 1984, Pierce & Elgar 1985, Sands 1986).

In all these cases adult appeasement substances might exist as postulated by Maschwitz et al. (1985a). Ovipositing females of *Anthene emolus* are first attacked by their host ant *Oecophylla smaragdina*, but after oviposition has commenced the ants remain calm, suggesting that the scent of the freshly laid eggs might function as an appeasement substance here (Fiedler & Maschwitz 1989b). In contrast, adults of the same lycaenid just eclosing from the pupa are killed as prey.

In at least one miletine species, *Allotinus unicolor*, the butterflies communicate with the ants in a tactile way using their proboscides (Fiedler & Maschwitz 1989c). The relationships of adult lycaenid butterflies towards ants and related adaptations apparently cover a wide range which needs further investigation until generalizations should be made.

Ecology of lycaenid-ant interactions

Two hypotheses, which are by no means mutually exclusive, have been proposed to explain the ecological role of lycaenid myrmecophily. According to the "defence hypothesis", originally proposed by Lenz (1917) and vigorously supported by Malicky (1969b, 1970a), the only selective advantage of myrmecophily is the ability to survive in habitats where aggressive ants are abundant. Malicky (1969b, 1970a), in particular, stated that attendant ants do not yield any protection against enemies to the caterpillars.

The "mutualism hypothesis", in contrast, implies that ant-associations reduce the mortality risk of caterpillars because attendant ants thrive away at least some parasitoids or predators. This hypothesis, of which Thomann (1901) was one of the earlier representatives, was experimentally proven for two lycaenid species by Pierce & Mead (1981), Pierce & Eastseal (1986), and Pierce et al. (1987). Occasional observations on *Anthene emolus* (Fiedler & Maschwitz 1989b), *Brephidium exilis* (Fernandez Haeger 1988) and others further indicate that attendant ants are able to deter part of a caterpillar's enemies.

The interactions between lycaenid larvae and ants range from indifferent coexistence to close and obligatory associations. Warnecke (1932/33), Hinton (1951) and Henning (1983a) have proposed ecological classifications of the Lycaenidae with regard to their life-histories. Since all these groupings are connected continously with each other, I here only give a short characterization of the main types of interactions. The reader is referred to the cited works for details.

The first group to mention are the myrmecoxenous species, i.e. those without a functional DNO (Kitching & Luke 1985). Such caterpillars are very rarely found in stable associations with ants, and their predominant selective advantage is to escape ant attacks. For myrmecoxenous lycaenids only the "defence hypothesis" holds true. Nevertheless, as has been discussed in detail by Lenz (1917), Malicky (1969b) and Atsatt (1981a), this is a highly significant selective advantage, because myrmecoxenous larvae have access to ecological niches where predatory ants limit or even preclude the existence of many other insects. In such niches fewer competitors and enemies exist, offering the caterpillars an "enemy-free space" (Atsatt 1981a).

The second ecological group within the Lycaenidae are the truly myrmecophilous species. Normally these myrmecophiles possess a DNO (and often TOs) and thus are able to secrete nutritive substances towards the ants. Myrmecophilous larvae are attended by ants, but the degree of myrmecophily is again extremely variable. Some species are only exceptionally ant-attended, presumably since they either produce less attractive secretions or live in habitats where contacts with ants seldom occur. Larvae of other species are, at least in later instars, nearly permanently visited by ants. Even more specialized are those lycaenids that are obligatorily associated with a particular host ant genus or species.

Although experimental evidence is currently available only for the two species studied by Pierce and one riodinid (see above), all such myrmecophilous associations of lycaenid caterpillars possessing a DNO are here basically viewed as mutualistic relationships on the following reasoning.

There are numerous examples that trophobiotic associations of homopterans with ants are mutualistic. Attendant ants gain substantial food resources and, in turn, defend their trophobionts (e.g. Way 1963, Messina 1981, Buckley 1987, 1990, Hanks & Sadof 1990, Olmstead & Wood 1990a). This protective effect may vary with ant species (Bristow 1984, Cushman & Addicott 1989), or with time and population density of the trophobionts ("conditional mutualism": Cushman & Whitham 1989).

A somewhat parallel situation exists in plants with extrafloral nectaries that attract ants; such plants are often protected by attendant ants against herbivores (e.g. Tilman 1978, Schemske 1982, Whalen & Mackay 1988, Rico-Gray & Thien 1989), although some studies failed to demonstrate such a protective effect (e.g. O'Dowd & Catchpole 1983).

Based on this evidence as well as the impressive experimental studies of Pierce and her coworkers on *Glaucopsyche lygdamus* and several *Jalmenus* species, it is feasible to assume that stable lycaenid-ant associations represent, in many cases at least, trophobiotic mutualisms, where the caterpillars receive some protection by the ants and reward the latter with nutritive secretions.

Recent studies have shown that caterpillar secretions may indeed contribute significantly to the nourishment of ant colonies (Pierce et al. 1987, Fiedler & Maschwitz 1988a, 1989b). As with the better known mutualisms between ants and plants or homopterans, the protective effect of such symbioses is never perfect.

Ant-plant mutualisms are exploited by herbivores adapted to the presence of ants (e.g. myrmecophilous lycaenid or riodinid caterpillars: Maschwitz et al. 1984, Horvitz & Schemske 1984, DeVries & Baker 1989, DeVries 1990b), and specialized predators invade ant-tended homopteran aggregations (e.g. lycaenid caterpillars of the subfamily Miletinae: Cottrell 1984, Maschwitz et al. 1985a, 1988, Ackery 1990; beetles and syrphid flies: Pontin 1959).

Thus, one cannot anticipate that the protective effect of attendant ants for myrmecophilous lycaenid caterpillars is significant under all circumstances, and the mere observation that myrmecophilous lycaenid caterpillars suffer from parasitism

does not disprove the mutualism hypothesis. Highly adapted parasitoids and predators as well as the ant species involved, the larval population density, and abiotic factors certainly shape and modify the selective outcome of any such association. Clearly this is a field open to further and more detailed research (e.g. Pierce 1989).

In addition, the balance of costs and benefits of myrmecophilous associations probably covers a wide range. When the selective pressure of parasitoids or predators is rather low, or if the caterpillars have alternative defensive strategies, they may produce few or rather unattractive secretions. Then they still retain the important advantage of not being preyed upon by the ants, while the ants receive little or no reward for their lack of aggressiveness. The other extreme are those lycaenids whose survival is impossible without ants due to heavy predation (e.g. *Jalmenus*: Pierce et al. 1987). Between these extremes lies a continuum of potential mutualistic interactions.

A third ecological category are the "parasitic" lycaenid-ant interactions, which can further be subdivided into two classes. Several lycaenid caterpillars destroy the food resources of ants by feeding upon myrmecophytes (Maschwitz et al. 1984) or trophobionts (Maschwitz et al. 1985a, 1988). Such competetive interactions have been termed "indirect parasitism" by Maschwitz & Fiedler (1988).

The larvae of some other lycaenids live inside ant nests where they prey on ant grubs or receive ant regurgitations (see Cottrell 1984 for review), thereby "parasitizing" on the energy budget of the whole ant colony. Again there is a wide spectrum with regard to the impact of the lycaenid larvae on their host ant colony.

Some "parasitic" caterpillars still pass attractive (and presumably nutritive) secretions to the ants (several Aphnaeini, *Acrodipsas*), others only participate in the social food exchange (*Euliphyra mirifica, Maculinea alcon, M. rebeli*), while a third group significantly decimates the immature stages of their respective host colonies (*Maculinea arion, Liphyra brassolis*).

Whether true commensalism as a fourth ecological category does exist among the Lycaenidae is still unclear. However, the larvae of several African Liptenini have apparently been found exclusively in the close vicinity of specific ant nests (Farquharson 1922, Jackson 1937), and these non-predatory larvae are thought to feed on fungi or debris and might thus be examples of true caterpillar-ant commensalisms.

So, the ecological interactions of lycaenid larvae and ants continously cover the wide range from indifferent coexistence, across facultative or obligatory mutualisms, to more or less severe parasitic (and possibly commensalic) interactions.

Aims of the present study

The fascinating phenomenon of myrmecophily has always attracted the attention of entomologists since the 18th century. The last decade brought considerable progress in the understanding of these interactions. Furthermore, the sociobiological paradigm generally stimulated the investigation and interpretation of mutualistic and parasitic systems.

Pierce and her coworkers, in particular, have proposed a number of far-reaching hypotheses regarding the ecology and evolution of lycaenid-ant interactions, mainly based on their experimental work on *Glaucopsyche* and *Jalmenus*. Other new questions arose from the studies of Fiedler & Maschwitz (1988a, b, 1989a).

The present work pursues a twofold aim. In the next main section I shall describe an experimental method to quantitatively analyse the behavioural interactions between lycaenid larvae and ants, with special reference to the function and importance of the various myrmecophilous organs. In particular, I shall examine the role of the DNO and the PCOs in some European species in order to test the findings of Fiedler & Maschwitz (1988a, 1989a) that the DNO is the critical organ for stable and truly mutualistic associations. The role of the myrmecophilous organs, and the distinction between myrmecophilous and myrmecoxenous species, have been insufficiently evaluated in many studies. This section on the experimental ethology of lycaenid-ant interactions is a complete essay for its own.

In the subsequent chapters I shall critically re-examine some of the evolutionary and ecological hypotheses proposed in the recent literature. In contrast to a purely sociobiological view, this re-examination is based on two fundamentals: a basically systematic approach, and a comprehensive and extensive compilation of as much information as available on lycaenid life-histories.

The third chapter gives a review of the modern systematics of the Lycaenidae and describes the trade-offs with myrmecophily. The existence of any such correlations between phylogeny and the myrmecophilous relationships within the Lycaenidae was hitherto rejected by Pierce & Elgar (1985) and Pierce (1987).

In the fourth chapter the specificity of lycaenid-ant interactions will be discussed, with special reference to the lycaenid taxa showing obligatory myrmecophily.

The fifth chapter summarizes the hostplant relationships of the Lycaenidae under a systematic aspect. In particular, the hypothesis of Pierce (1985) that myrmecophilous caterpillars preferentially feed on nitrogen-fixing hostplants is compared with data for more than 1000 lycaenid species.

In the following chapter I describe and analyse the biogeographical patterns of myrmecophily, and the final chapter is devoted to the proposal of some hypotheses concerning the evolution of lycaenid-ant interactions.

This second and main part of the present monograph is basically a comparative, non-experimental study in evolutionary biology. It is founded on data concerning the larval biology and myrmecophily of nearly 1070 lycaenid species. These records, summarized and arranged in tables in the Appendix, were extracted from more than 300 literature sources and include numerous unpublished observations kindly communicated by colleagues.

In face of the tremendously scattered and steadily expanding entomological literature, the database presented is certainly not exhaustive. A considerable amount of informa-

tion on larval hostplants or ant-associations is certainly still hidden in faunistic or rearing reports, often published in only locally distributed journals.

Furthermore, it was impossible to check all old records by myself, and in these cases I must rely on the excellent reviews by Warnecke (1932/33), Hinton (1951), Malicky (1969b), or Cottrell (1984). Notwithstanding, the tables present the most complete compilation of relevant information concerning the larval biology of the Lycaenidae that has yet been published, and the main conclusions drawn from this database should, despite the still significant gaps in our current knowledge, prove reliable.

On this background of a broad "classical" comparative and systematic survey, the present monograph is intended to provide a complement to the sociobiologically and ecologically reasoned hypotheses, which have so markedly stimulated the recent research on the biology and evolution of the Lycaenidae, but currently tend to dominate the discussion. The final goal is an evolutionary synthesis of these two approaches.

BEHAVIOURAL INTERACTIONS BETWEEN LYCAENID LARVAE AND ANTS: A COMPARATIVE EXPERIMENTAL STUDY

The use of quantitative methods in the investigation of myrmecophily

As pointed out above, presence and function of the myrmecophilous organs of lycaenid caterpillars play essential roles in the outcome of encounters with ants. The experiments of Fiedler & Maschwitz (1988a, b, 1989a) strongly indicate that the morphological distinction between myrmecoxenous caterpillars with only PCOs present, and myrmecophilous larvae possessing an additional DNO (and often a pair of TOs), has a behavioural as well as an ecological correlate.

Larvae with a functional DNO are generally more attractive to ants, and they are able to release food recruitment behaviour in ants, thereby inducing stable associations that may be further enhanced by the use of the TOs or vibrational communication. Hence, such larvae are much more likely to be attended by ants in the field.

This view, however, contradicts the findings of Malicky (1969b). According to him all lycaenid caterpillars are treated by appropriate ants in basically the same way, the large variability observed not being correlated with the presence or absence of the DNO or TOs. Furthermore, Malicky denied differences between caterpillars with or without a DNO regarding ant-associations in the field. To decide this controversy, it is thus necessary to investigate the behavioural interactions between caterpillars and ants in more detail.

In the following I describe a quantitative method for comparing lycaenid-ant interactions. As Malicky's experiments were not intended to yield quantitative data for statistical evaluations, a direct comparison with his results is possible to only a limited degree. The single other quantitative study available is that of Ballmer & Pratt (in press) on Californian lycaenids (see discussion).

Although recruitment experiments proved the existence of one important difference in the behaviour of ants towards myrmecophilous and myrmecoxenous caterpillars (Fiedler & Maschwitz 1989a), such experiments have considerable practical disadvantages:

First, the willingness of ants to perform food recruitment largely depends on the nutritive status of the colony as a whole. It is difficult and time-consuming to assess this status and even more problematic to warrant standardized experimental conditions.

Secondly, the number of ant workers in a colony and the number of ants that engage in foraging may provide a source of great variance. Even using the same ant colony all the time does not rule out such differences.

Thirdly, recruitment trials have to last considerable time; e.g. with the ant *Tetramorium caespitum* an experimental duration of one hour was found to be necessary (Fiedler & Maschwitz 1989a).

Hence, only a limited set of data can be sampled per day. Given the difficulties of breeding lycaenid caterpillars and the often short and unpredictable availability of ap-

propriate instars, I thus decided to develop a more standardized and easily replicable experimental method to allow quantitative comparisons for at least a small range of species.

Material and methods

Larvae of the only European riodinid *Hamearis lucina* L., 1758 and of 7 European lycaenid species were examined. The latter were: 3 myrmecophilous *Polyommatus* species (*coridon* Poda, 1766; *icarus* Rottemburg, 1775; and *escheri* Hübner, 1823), 3 *Lycaena* species without a DNO (*phlaeas* L., 1761; *tityrus* Poda, 1766; and *hippothoe* L., 1761), and *Callophrys rubi* L., 1758 whose larvae possess a DNO, but no TOs. *H. lucina* is myrmecoxenous, too (cf. Malicky 1969a).

This range of species covers three of the five tribes of the Lycaeninae, namely Lycaenini, Eumaeini, and Polyommatini. *H. lucina* belongs to the subfamily Hamearinae. The latter taxon retains a number of plesiomorphic traits and is thus viewed as the most primitive subfamily of the lycaenids' presumed sister-family Riodinidae (Harvey 1987). Unfortunately, no representatives of the tropical subfamilies Curetinae, Miletinae and Poritiinae, and no species of the Lycaeninae tribes Aphnaeini and Theclini were available.

P. icarus, the *Lycaena* species, *C. rubi* (in part), and *H. lucina* were reared from eggs obtained from captive females, while *P. coridon, P. escheri* and *C. rubi* (in part) were collected as 2nd or 3rd instar larvae. The rearing method largely followed Schurian (1989a), modifications for single species were given by Fiedler (1989a, 1990a, d, e).

For experiments only final instar larvae (i.e. 4th instars in all species examined) were used. Two ant species from different subfamilies were employed, viz. *Tetramorium caespitum* (Myrmicinae) and *Lasius flavus* (Formicinae). Colonies of both were kept in earth nests in a greenhouse under nearly ambient conditions and were fed honey-water and cockroaches as needed.

For experiments, 25 (*L. flavus*) or 50 (*T. caespitum*) worker ants were taken from the colonies and put into clear plastic boxes (10 x 10 x 6 cm). A transparent lid prevented the ants from escape. The larger ant number with *T. caespitum* reflects the smaller size and lower activity of this species when compared with *L. flavus*.

Only ants freely foraging in their nest containers were used to ensure that they would readily display trophobiotic behaviour when encountering the caterpillars. The ants then were left undisturbed until they had calmed down for at least 10 min. Subsequently, two mature lycaenid larvae (usually belonging to the same species) were carefully introduced, and the behaviours of the caterpillars and ants were observed for 30 min.

Every 30 s the number of ants actually associated with each caterpillar was recorded, and the visits of ants at the DNO, the DNO secretion rates and eversions of the TOs were counted throughout. An ant was considered as associated with a caterpillar if it was either sitting on the latter, or if it had antennal contact to the larva.

After 30 min the caterpillars were removed, and the ants were left undisturbed for at least 15 min until the next test with two new larvae took place. The same group of ants was never used for more than three successive trials, since after 1—2 h of separation from their nests most ants showed reduced activity or otherwise abnormal behaviour. All experiments were conducted at 22—26 °C with indirect daylight in a southwest-facing room between 10.00 and 18.00 CEST. Every 7.5 min the experimental box was rotated by 90° to avoid any bias through possible preferences of ants or caterpillars for the darker or brighter corners.

In several larvae of *Polyommatus coridon* and *P. icarus* the DNO was covered with a cap of glue (UHU schnellfest plus™) in order to investigate whether this exclusion of the DNO resulted in a detectable change of the behaviours of attendant ants. This treatment had no adverse effects on the caterpillars and all pupated and eventually produced sound adults.

The influence of larval hostplants on the myrmecophilous qualities of *P. icarus* caterpillars, as measured in experiments of the same design, has already been reported in detail (Fiedler 1990a, c).

The observational data were used to calculate the following myrmecophily parameters:

1.) Larval attractiveness, **A:** the mean number of ants attending each larva;
2.) Relative variablity of attractiveness, **RV:** the standard deviation of A divided by A (this quotient is usually termed coefficient of variation: Sachs 1978);
3.) Permanence of ant-association, **P:** the number of counts when a larva was attended by at least one ant, divided by the total number of counts (i.e. divided by 30 for 15-min trials).

These parameters as well as the secretion and eversion rates of the DNO or TOs, respectively, were then statistically evaluated using the non-parametric U-test of Mann & Whitney (Caradoc-Davies 1985).

A preliminary survey showed that *L. flavus* (which was the distinctly more active ant species) tended to visit caterpillars most intensively during the first half of the 30-min experiments, while the reverse was true for *T. caespitum*. Thus, in order not to underestimate the attractiveness of the lycaenid larvae, the parameters A, RV and P were calculated separately for the first and second half of each 30-min trial.

For further analyses the first-half values were used with *L. flavus* and the second-half values with *T. caespitum*. A parallel evaluation of the combined data did not yield different results with regard to significance of interspecific differences.

Ballmer & Pratt (in press), for their different approach to measure the permanence of ant-associations, present their percentage data in an arcsine-transformed manner. To facilitate direct comparisons, all figures for P obtained in this study are thus additionally given in the same transformation.

Results

Myrmecophilous species

P o l y o m m a t u s   c o r i d o n — Caterpillars of *P. coridon* were always intensively palpated by both ant species and usually received permanent attention. The ants' in-

terest concentrated upon the DNO and the spiracles, and on numerous occasions the ants were observed to nibble at the PCOs, presumably harvesting their secretions. Aggressive behaviours of the ants (biting, stinging, spraying of defensive secretions) were never observed.

The larvae showed no signs of being disturbed by the ants and often walked through the experimental box carrying several ants on their backs. Even when a caterpillar fell off the side-parts of the box, the ants never responded aggressively, but with a short increase in their locomotion activity at most.

The release of DNO secretion droplets was commonly observed, but due to the almost continous presence of ants around the DNO the exact secretion rates could not be established with certainty. Fiedler & Maschwitz (1988a) have reported secretion rates of 15-74 droplets/h (mean 31 droplets/h) when observing *P. coridon* larvae under a stereo microscope.

In the experiments with the ant *L. flavus*, the DNO was on average intensively palpated 20.79 times (S.D. = 5.12) in 15 min. In the same trials, the TOs were everted with a mean rate of 24.13 per 15 min, but with a considerable higher variance (S.D. = 12.69). While in 4 cases more than 40 eversions were observed, 2 larvae used their TOs less than 10 times.

L. flavus worker ants regularly responded to contacts with everted TOs displaying excited runs as described by Elfferich (1965) and Fiedler & Maschwitz (1988b), while ants of the myrmicine species *T. caespitum* did never.

The myrmecophily parameters A, RV and P of *P. coridon* larvae were significantly different from all other lycaenid species tested with *L. flavus* (see Tab.2a). With *T. caespitum* the attractiveness A of *P. coridon* caterpillars was again significantly higher than that of the other lycaenids investigated, while the parameters RV and P were similar to those of the 2 further *Polyommatus* species, but different from the values obtained with the myrmecoxenous larvae (Tab.2b).

During the experiments the caterpillars often produced faecal pellets (usually one per larva and trial). In four out of 24 occasions, 1—3 (maximum 6) ants of the species *L. flavus* intensively chewed and sucked at the fresh pellets for several minutes, but without reducing the ant-association of the larva itself. *T. caespitum* showed no interest in the caterpillar frass.

Exclusion of the DNO (only tested here with the ant *L. flavus*) significantly influenced the behaviour of ants towards the larvae. The attractiveness of the larvae was reduced to less than half the figure of intact caterpillars, while RV increased by about 50 %. The strongest effect was observed at the DNO itself: the DNO region was on average only palpated 2.86 times (S.D. = 2.49) in 15 min, i.e. about 10 % of the figure observed with intact larvae. The cap of glue had no noticeable deterrent effect on the ants; the ants were simply no more attracted to the DNO. The reduction of the permanence of the ant-associations was less distinct, but still highly significant.

The function of the TOs, however, was not significantly affected (mean eversion rate = 20.82, S.D. = 8.43). Clearly, the exclusion of the DNO rendered *P. coridon* caterpillars less attractive to ants with a more fluctuating and less stable ant-association, but they remained ant-attended to a considerable degree (Tab.2a).

P o l y o m m a t u s   i c a r u s — Caterpillars of this species were treated by both ant species in a way similar to that observed with *P. coridon*, but intensive palpation was more markedly restricted to the DNO and to the PCO accumulations at the spiracles. No aggressiveness of the ants was ever observed, and the caterpillars often calmly walked about carrying ants on their backs.

However, the myrmecophily parameters of *P. icarus* caterpillars significantly differed from those of *P. coridon* (all data regarding *P. icarus* refer to larvae reared on herbaceous Fabaceae, see Fiedler 1990a, c). Their attractiveness was only about one third with both ant species, and in the experiments with *L. flavus*, larvae of *P. icarus* had more fluctuating and less permanent ant-associations than *P. coridon* caterpillars (Tab.2a).

Important differences were observed with regard to the function of the myrmecophilous organs. *L. flavus* ants palpated the DNO on average 26.35 times in 30 min, but with a high variance (S.D. = 16.32). This rate, when compared with the 15-min figure of *P. coridon* (20.79), indicates a distinctly lower attractiveness of the DNO in *P. icarus*. *T. caespitum* ants palpated the DNO of *P. icarus* with a similar mean frequency (28.21 ± 21.85 in 30 min). This same ant species usually attends the DNO of *P. coridon* caterpillars so constantly that it is nearly impossible to count distinct palpation events.

In *P. icarus* larvae DNO secretions were only observed within the last 2 days of the ultimate larval instar, and in trials with *T. caespitum* the actual secretion rate was low and rather unpredictable even then (2.68 ± 2.86 droplets/30 min), yielding an estimated mean rate of 5—6 droplets/h (*P. coridon*: 31 droplets/h).

The frequency of intensive palpation at the DNO was highly significantly correlated with all 3 myrmecophily parameters (experiments with *L. flavus*; Spearman's rank correlation; A: r_S = 0.60, RV: r_S = -0.64, P: r_S = 0.66; p < 0.001, n = 26), which indicates that the activity of the DNO is the main factor governing the ant-associations of *P. icarus* larvae.

Regarding the activity of the TOs, again important differences were found between *P. icarus* and its congener *P. coridon*. With both ant species tested the eversion rates of the TOs were equally low and highly variable in *P. icarus* (*L. flavus* [30 min]: 5.96 ± 8.01; *T. caespitum* [30 min]: 6.84 ± 8.95). In only 16 out of 90 experiments TO eversion rates of 15—40/30 min were observed, while in 28 trials the caterpillars did not use their TOs at all.

As with *P. coridon*, only the ant species *L. flavus*, but not *T. caespitum* responded to contacts with everted TOs by the typical excited runs, although this reaction was usually less pronounced. Nevertheless, there was a significant correlation between the eversion rate of the TOs and the parameters P (Spearman's rank correlation coefficient r_S =

0.56, p < 0.002, n = 26) and RV (r_S = -0.52, p < 0.002), suggesting that the TOs indeed enhance the stability and permanence of larval ant-associations as proposed by Fiedler & Maschwitz (1988b). Larval attractiveness or the frequency of intensive stimulation of the DNO, in contrast, were not significantly correlated with the activity of the TOs.

The caterpillars regularly produced faecal pellets during the experiments. *L. flavus* responded to the fresh frass in 13 of 26 occasions with intensive chewing and sucking. Within 5 min the pellets became thus literally dry and shrimpeled. On at least two occasions the pellets were immediately taken by worker ants from the larval anus. *T. caespitum* showed no interest in the frass. Preliminary tests with the ninhydrine reagent proved the presence of considerable amounts of amino acids in the frass.

P. icarus caterpillars, albeit significantly less myrmecophilous than the congeneric *P. coridon*, received distinct attention by ants and regularly induced rather stable ant-associations. This was no longer the case when their DNO was rendered unfunctional (experiments with *L. flavus*). Covering the DNO with a cap of glue led to a complete breakdown of their ant-association (Tab.2a).

Ants then only sporadically visited the larvae for short times, and intensive palpation was hardly ever observed. The DNO was visited on average only 9.70 times (S.D. = 7.48) in 30 min, and usually the ants soon left it. Attacks did never occur, but the ants took very little interest in the caterpillars.

Unfortunately, in these experiments the TOs were likewise actually excluded, since no larva was seen to use its TOs during the trials. Apparently the cap of glue precluded the eversion mechanism of the TOs, possibly because in the smaller caterpillars of *P. icarus* the edges of the DNO cap were too close to the TOs' sheath.

Thus, the strong reduction of the caterpillar-ant interactions might be due to the combined loss of both DNO and TOs. However, in feeding experiments with *P. icarus* on a nutrient-poor diet (*Robinia pseudoacacia*) a likewise drastic decline in myrmecophily was observed although the TOs remained fully functional there (Fiedler 1990c).

Polyommatus escheri — The few data obtained with only five individuals of this Mediterranean species permit just limited evaluation, even more so because the larvae were reared under a severe shortage of food. They did not accept any of several representatives of the family Fabaceae (*Onobrychis, Medicago, Hippocrepis, Trifolium*) as a substitute for their natural hostplant (*Astragalus monspessulanus* and allies) which was not sufficiently available. Given these premises, and in view of the finding that in *P. icarus* a sufficient larval nutrition is essential for the maintenance of ant-associations, the following data obviously represent nothing more than lower limits for the myrmecophily parameters of *P. escheri*.

Ants (*T. caespitum*) palpated the *P. escheri* caterpillars intensively, especially around the DNO. No attacks were observed. Three trials were made when the larvae were already in the prepupal stage and were thus no more able to evert their TOs or release secretions from the DNO.

The other five experiments yielded results somewhat intermediate between the two other *Polyommatus* species investigated (*coridon, icarus*; see Tab.2b). The mean frequency of palpation at the DNO within 30 min was rather low (13.60 ± 8.64, median = 18), and this may be attributed to the inability of the larvae to produce DNO secretions without appropriate food.

The eversion rate of the TOs, in contrast, was distinctly higher than in *P. icarus* (22.0 ± 14.35, median = 19). The myrmicine ant *T. caespitum*, however, showed no reaction on contacts with everted TOs. One larva successfully pupated during an experiment with constant attendance of 3—10 ants immediately before and after the moult.

Myrmecoxenous species

L y c a e n a   p h l a e a s — Both ant species tested normally behaved peacefully towards caterpillars of *L. phlaeas*. However, most contacts lasted rather short and the ants usually only groped the larvae instead of typically palpating them (this distinction between groping [*Betasten*] and palpation [*Betrillern*] follows Malicky 1969b, 1970a). Real palpation was only occasionally observed and it normally waned soon, in particular with *L. flavus*. The ants' interest concentrated upon the PCO accumulations around the spiracles, especially on the prothorax and the 6th—8th abdominal segment. There the ants often nibbled with their mandibles, presumably harvesting the secretions.

Larvae of *L. phlaeas* only partially induced rather stable ant-associations (in 4 out of 16 trials with *L. flavus* and in 12 of 17 trials with *T. caespitum*). In 6 of 16 trials with *L. flavus* and in 1 of 17 with *T. caespitum*, individual ants tried to bite the caterpillar, but did not hurt it. Larvae thus attacked retracted their head under the prothoracic shield and repeatedly lifted their fore or rear end briefly, but showed no stronger defensive reaction (e.g. true thrashing).

Generally the myrmecophily parameters of *L. phlaeas* were significantly different from those of the *Polyommatus* species, with the single exception of larval attractiveness in experiments with *T. caespitum* (Tab.2).

L y c a e n a   t i t y r u s — Experiments with this species yielded very similar results. Indeed, the quantitative figures are in no case significantly different from those of *L. phlaeas* (Tab.2). As with the latter species, caterpillars of *L. tityrus* were mostly groped and only occasionally palpated.

Stable ant-associations were observed only twice in 14 experiments with *L. flavus*, but in 4 of 6 trials with *T. caespitum*. Faecal pellets produced by the caterpillars were highly attractive to *L. flavus*. Regularly 2—6 (maximum 12) ants chewed on such frass. On four occasions the frass received higher attendance than the larva itself, and ants were observed to leave the caterpillars to suck at their fresh faeces. The frass contained high amounts of amino acids (ninhydrine test).

L y c a e n a   h i p p o t h o e — Caterpillars of this third *Lycaena* species were more intensively palpated than the two others, especially the large mature larvae. The latter

induced even stable ant-associations, but the larvae repeatedly showed defensive movements (brief lifting of fore or rear end) and retracted their head, or they even rolled up completely when visited by more than five ants.

Small younger last instars of *L. hippothoe*, in contrast, were treated in essentially the same way as caterpillars of *L. phlaeas* and *tityrus*. The combined data for all trials with *L. hippothoe* largely agree with those of the two other *Lycaena* species (Tab.2a).

The comparatively large faecal pellets (length 2—3 mm, $\varnothing = 1$ mm) were extremely attractive to *Lasius flavus* ants. Six of eight frass pellets were chewed upon by 2—5 (maximum 15) ants, in one case for at least 22 min.

Callophrys rubi — Larvae of this member of the tribe Eumaeini were treated distinctly more aggressively by both ant species than *Polyommatus* or *Lycaena* caterpillars. *T. caespitum* never showed typical palpation, but brief groping at most, and *L. flavus* only very occasionally palpated *C. rubi* larvae for short periods. In 12 of 21 trials with *T. caespitum* and in 5 of 26 experiments with *L. flavus* some ants repeatedly tried to bite the *C. rubi* larvae. Twice a *T. caespitum* worker ant tightly clinged to a caterpillar for several minutes and even attempted to sting. In all these cases the caterpillars responded with defensive movements (brief lifting of the fore end, retraction of the head) and remained unhurt.

Although *C. rubi* larvae possess a DNO, no ants were ever observed to be attracted to this and actually I could never observe any DNO secretions. In summary, the larvae of *C. rubi* were very unattractive to both ant species and even rather often attacked. Their myrmecophily parameters were predominantly similar to those of the myrmecoxenous *Lycaena* species or even lower in part (Tab.2).

The frass pellets of *C. rubi* were highly attractive to *L. flavus* ants; 11 of 14 pellets were immediately visited by ants, whereas only three received no interest. On two occasions the ants took the frass directly from the larva's anus, and four faecal pellets were attended for 21—28 min.

Hamearis lucina — The larvae of *H. lucina* were totally unattractive to ants (tested only with *L. flavus*), but were regularly attacked. The ants tried to bite the larvae and exhibited a defensive posture after the first contacts.

Such attacks of *Lasius* ants against *H. lucina* larvae were already noted by Malicky (1969b). Several ants sat around one caterpillar with the mandibles opened and the gaster bent forward beneath the thorax. Even spraying of formic acid was confirmed on several occasions by its characteristic odour. Generally, the ants showed signs of alertness at the beginning of all experiments with *H. lucina*, but after the initial 5—10 min the larvae were largely ignored.

Caterpillars of this riodinid species differ from the lycaenids investigated in their dense coating with rather long and stiff hairs. Therefore the attacking ants were unable to hurt the caterpillars and when they grasped the ends of the long bristles, these were immediately released. In addition, the larvae showed defensive movements (short shaking of the head) and quickly crawled away when the ants became too harassing.

H. lucina caterpillars were the most active of all species tested, and their myrmecophily parameters were the lowest. In 7 of 11 cases the faecal pellets received considerable attendance of 1—8 ants for up to 10 min. The frass was in all these cases distinctly more attractive than the larva itself.

Tab.2: Quantitative results of experiments on interactions between caterpillars and ants. Given are means (standard deviations in parentheses). A: attractiveness of larvae; RV: coefficient of variation of A; P: permanence of ant-association; PT: arcsine-transformed values of P (definitions see text); n: number of experiments. -DNO: dorsal nectary organ of larvae rendered unfunctional. Figures of each column followed by different letters are statistically different (Mann-Whitney U-test, p < 0.05).

a) Experiments with *Lasius flavus*

	A	RV	P	PT	n
Polyommatus coridon	6.37 (1.59)a	0.061 (0.021)a	1.00 (0)a	90.00 (0)	24
P. coridon (-DNO)	2.77 (1.26)b	0.096 (0.038)b	0.93 (0.11)b	79.31 (12.02)	28
P. icarus	1.78 (0.82)c	0.152 (0.149)c	0.79 (0.17)c	66.31 (15.06)	26
P. icarus (-DNO)	0.65 (0.54)e	0.329 (0.146)e	0.41 (0.24)e	39.43 (14.94)	20
Lycaena phlaeas	1.36 (1.00)d	0.210 (0.062)d	0.59 (0.18)d	50.61 (11.45)	16
L. tityrus	0.91 (0.75)de	0.278 (0.145)de	0.51 (0.26)de	46.82 (18.88)	14
L. hippothoe	1.97 (2.10)cd	0.236 (0.177)cd	0.63 (0.33)d	57.11 (25.46)	17
Callophrys rubi	0.81 (0.59)e	0.290 (0.165)de	0.45 (0.23)e	41.80 (14.77)	26
Hamearis lucina	0.62 (0.33)e	0.263 (0.085)e	0.43 (0.17)e	41.00 (10.46)	24

b) Experiments with *Tetramorium caespitum*

	A	RV	P	PT	n
Polyommatus coridon	10.16 (2.23)a	0.063 (0.009)a	0.99 (0.02)a	88.72 (4.43)	12
P. icarus	3.89 (2.55)b	0.079 (0.054)a	0.94 (0.15)a	83.22 (13.98)	38
P. escheri	3.35 (2.32)b	0.095 (0.056)b	0.92 (0.16)ab	80.37 (15.61)	8
Lycaena phlaeas	3.14 (2.69)b	0.118 (0.061)b	0.84 (0.19)b	71.64 (17.24)	19
L. tityrus	2.46 (1.54)b	0.144 (0.105)b	0.79 (0.32)b	72.67 (26.91)	6
Callophrys rubi	2.57 (1.50)b	0.118 (0.068)b	0.84 (0.22)b	74.39 (19.59)	21

Discussion

The function of the myrmecophilous organs

P o r e   c u p o l a   o r g a n s   (P C O s) — The above experiments yielded additional information about the role of the three major types of myrmecophilous organs found on lycaenid larvae. With regard to the PCOs, it is apparent that these organs are attractive to ants in the genera *Polyommatus* and *Lycaena*, but not in *Callophrys rubi* and *Hamearis lucina*. The latter two species were rarely if ever palpated at their PCOs.

These findings quantitatively confirm the qualitative statement of Malicky (1969b) that considerable differences exist in the attractiveness of lycaenid immatures to ants. The

most likely explanation of such differences is that the PCO-secretions of the species investigated differ in their chemical composition. The low attractiveness of *C. rubi* and *H. lucina* larvae even raises the question as to whether the PCOs of these species release any ant-related secretions at all, and generalizations regarding the function of the PCOs and their secretions should thus be seen with caution. DeVries (1988) and Harvey (1989) could not detect any attractiveness of the PCOs of several riodinids.

Thus, although it is currently generally accepted that the PCOs play an important role in the avoidance of ant-attacks (Malicky 1969b) or even serve as attractive glands with possibly nutritive secretions (Pierce 1983, 1989), this view urgently needs substantiation by chemical investigations on a broader spectrum of species. Obviously, the ant-attracting or appeasing function of the PCOs is not a universal trait common to both the Riodinidae and Lycaenidae, but is restricted to one subfamily, viz. the Lycaeninae.

The PCOs even differ in their attractiveness to ants among related species, or among individuals of the same species. *P. coridon* larvae were always palpated much more intensively than those of *P. icarus*, and in the DNO-exclusion experiments *P. coridon* larvae still induced ant-associations, whereas *P. icarus* did not. In the recruitment experiments of Fiedler & Maschwitz (1989a) with *P. coridon*, caterpillars with a capped DNO likewise partially retained their attractiveness and released a weak residual recruitment response.

Solicitation of weak food recruitment was also observed with *P. coridon* pupae that only possess PCOs (Fiedler 1988a, Fiedler & Maschwitz 1989a). Pupae of *P. icarus* and *P. escheri*, too, were steadily palpated and decidedly attractive to ants (Fiedler, unpublished), and several *Polyommatus* species (e.g. *coridon, bellargus, icarus*) are known to be associated with ants (mainly of the genus *Lasius*) during the pupal stage in the field (Thomas 1983, Emmet & Heath 1990). All these observations suggest that species- and instar-specific, or even individual differences of the PCO-secretions do occur amongst the genus *Polyommatus*.

Within the genus *Lycaena* the results are likewise indicative of a variable attractiveness of the PCOs. In all three *Lycaena* species investigated, some larvae induced rather stable ant-associations while others did not. Large caterpillars of *L. hippothoe* were nearly always attractive, but in *L. tityrus* and *L. phlaeas* the attractiveness was usually rather low.

Corresponding results have been obtained with other species of *Lycaena*. Malicky (1969b) noted, without reporting quantitative details, that caterpillars of *L. virgaureae* and *L. dispar* were often attractive to ants. In his experiments *L. phlaeas, L. tityrus* and *L. hippothoe* were only weakly attended by ants. Elfferich (1963b, and pers. comm.) found caterpillars of *Lycaena dispar* and *L. ottomanus* attractive to the ant *Lasius niger*, whereas a *Myrmica* species showed no interest. Again *Lycaena phlaeas* and *L. tityrus* were usually unattractive. In addition to the results reported above I have observed strong palpation behaviour and permanent associations in laboratory trials with fully grown caterpillars of *Lycaena alciphron* and the ant *Lasius brunneus*.

The pattern thus emerging is that a number of *Lycaena* species have the potential to attract ants to some degree with the help of their PCOs, but that this attractiveness is

not realized in all individuals. As a consequence, ant-associations of *Lycaena* larvae have only occasionally been observed in the field (from Europe there are only single records for *L. dispar*: Hinton 1951, Ebert & Rennwald 1991). In four myrmecophilous *Lycaena* species from North America additional attractive organs (viz. dendritic setae) are involved (Ballmer & Pratt 1988, and in press).

Anyway, the PCOs apparently permit a fine tuning of the attractiveness of lycaenid caterpillars towards ants without major changes in morphology. The mechanisms underlying this intrageneric or even intraspecific variability require further study.

D o r s a l   n e c t a r y   o r g a n   (D N O) — The exclusion experiments confirmed the paramount importance of the DNO for the maintenance of stable ant-associations. *Polyommatus coridon* and *P. icarus* caterpillars with their DNO rendered unfunctional received distinctly less attention by ants, and the latter became even functionally myrmecoxenous. This finding contradicts the work of Malicky (1969b) who performed similar exclusion experiments, but could not observe differences in the ant behaviour following DNO-exclusion. This is clearly one aspect where the use of quantitative comparative studies provided a significant progress: without a statistical treatment the differences are sometimes difficult to detect.

As with the PCOs, the experiments revealed a considerable disparity in the function of the DNO between *P. coridon* and *P. icarus*. *P. coridon* caterpillars produce DNO secretions steadily throughout their 3rd and 4th instar at an average rate of about 30 droplets/h when mature. The palpation intensity at the DNO was rather similar with all larvae tested, suggesting that the secretory activity of *P. coridon* caterpillars of similar age varies little. *P. icarus*, in contrast, produced significantly fewer DNO secretions with an estimated rate of about 6 droplets/h. In addition, such secretions were regularly seen only during the last 2—3 days prior to pupation. Younger larvae (e.g. 3rd instars) very rarely released DNO secretions and accordingly they were even less intensively visited (Fiedler, unpublished).

Furthermore, the higher variance of the palpation frequency at the DNO indicates that the activity of this organ is much more variable in *P. icarus* larvae than in *P. coridon*. Differences in the nutritive quality of the actual larval hostplant could be partly responsible for this variability (Fiedler 1990c, Baylis & Pierce 1991).

In *P. icarus* the DNO-palpation frequency was significantly correlated with the myrmecophily parameters A, RV, and P (experiments with *L. flavus*; A: $r_S = 0.60$; RV: $r_S = -0.64$; P: $r_S = 0.664$; $p < 0.001$). In other words, larvae with an attractive DNO had the highest overall attractiveness and thus maintained stable and permanent ant-associations. In *P. coridon* no such correlations were found.

This is a further piece of evidence that a functional DNO is essential for the myrmecophily of *P. icarus*. Remarkably the caterpillars of *Callophrys rubi*, although possessing a DNO, were totally unattractive for both ant species. Indeed, no single secretion act could be observed with these larvae, and morphological examinations with the SEM revealed that most likely the DNO of *C. rubi* is rudimentary (Fiedler 1990d).

Malicky (1969b) has already noted that in some Eumaeiti larvae the DNO appears to be non-functional (e.g. *Strymon melinus, Satyrium acaciae*), and Ballmer & Pratt (in press) could not observe DNO secretion acts in 18 Californian species of the same subtribe.

This indicates that in some Eumaeiti the myrmecophilous organs show a marked tendency towards reduction, a character that will be discussed in detail later on. An important corollary of this findings is that it does not suffice to simply determine the presence or absence of the DNO in order to distinguish between myrmecophilous and myrmecoxenous species. This approach of Kitching & Luke (1985) has to be modified in that only lycaenid caterpillars with a **functional** DNO are likely to be attended by ants in the field.

Tentacle organs (TOs) — The experiments with *Polyommatus coridon* and *P. icarus* confirmed that the TOs of these species are able to alert certain formicine ants like *Lasius flavus* whereas the myrmicine ant *Tetramorium caespitum* showed no reaction. For both *Polyommatus* species this had been observed earlier (Elfferich 1963b, Fiedler & Maschwitz 1988b).

The TOs of *P. coridon* were more effective, and caterpillars of this species also evert their TOs more frequently than *P. icarus*. Apparently the signal produced by *P. icarus* is weaker than that of *P. coridon*. According to Elfferich (1963b) caterpillars of *P. icarus* elicit excited runs more effectively in the ant *Lasius niger* than in *L. flavus*.

As suspected earlier (Fiedler & Maschwitz 1988b), the eversion rate of the TOs was indeed significantly correlated with the permanence of associations between *P. icarus* larvae and *L. flavus*, supporting the view that the TOs may enhance and modify ant-associations of lycaenid caterpillars in general.

Another interesting observation was that the TOs rapidly loose their ability to alert ants when extruded for a longer time (more than 20 s). Usually everted TOs are detected or touched by attendant ants within seconds and are then immediately retracted. In DNO-exclusion experiments with *P. icarus*, however, the larvae had so little ant-attendance that sometimes a TO remained everted for up to one minute. When an ant encountered such a long-everted TO, it did not react at all and the TO was eventually retracted.

This observation indicates that the TOs may release a volatile signal that quickly evaporates. Similar results were obtained by Ballmer & Pratt (in press) with the North American *Plebulina emigdionis*. Caterpillars of this species often crawl about with everted TOs for several minutes, and ants (*Formica pilicornis*) are not alerted then. The same ant species readily reacted upon contact with the TOs of a number of related Californian *Plebejus* species.

It remains unknown whether the dendritic hairs on the top of the TOs produce and release the presumed volatile signal or simply serve as dissipative structures. In the latter case the allomone might be produced in the sheath of the TOs, and this could explain why Malicky (1969b) did not find glandular elements on the TOs.

Anyway, these observations are in accordance with the hypothesis that ant alarm-pheromones or mimics of those might be released by the TOs. Alarm-pheromones of ants are usually blends of multiple components (e.g. Bradshaw et al. 1979), and often one such component is used in a rather wide taxonomic range of ants (Hölldobler & Wilson 1990). This would explain why formicine ants of the genera *Lasius* or *Plagiolepis* respond to the TOs of *Polyommatus* caterpillars, whereas myrmicine ants like *Myrmica* and *Tetramorium* do not.

However, the reaction of *Tapinoma* ants (Dolichoderinae) to the TOs of *Polyommatus (Lysandra) golgus, P. nivescens*, and *Aricia morronensis* (Munguira & Martín 1988, 1989b) does not fit well into this hypothesis since the alarm substances of *Tapinoma* are chemically quite different (Hölldobler & Wilson 1990). Detailed investigations on the chemical nature of the signals produced by the TOs are clearly needed to further test the alarm-pheromone hypothesis, even more so since Malicky (1969b) has strictly rejected any glandular function of the TOs.

Comparative aspects

The quantitative investigations of the interactions between several European lycaenids and two ant species yielded one consistent result: the myrmecophily parameters differed significantly between myrmecophilous and myrmecoxenous caterpillars. This distinction was hitherto based mainly on the occurrence of the DNO and the presence of records of ant-associations in the field (Kitching & Luke 1985).

The existence of stable ant-associations in the field is unambiguously the ultimate and ecologically relevant criterion in this distinction. However, such final designations require thorough and time-consuming field work that has been done for far less than 50 lycaenid species from genera like *Lycaena, Jalmenus, Ogyris, Callophrys, Glaucopsyche, Maculinea, Plebejus, Polyommatus* (e.g. Wright 1983, Thomas 1983, 1985a, b, Thomas et al. 1989, Pierce & Elgar 1985, Pierce et al. 1987 etc.). Furthermore, field records are available only for a limited number of species and many records, for tropical species in particular, are based on single rearings or field observations, such data usually not permitting any direct comparisons.

Even in the better known European fauna, sufficient life-history information is available for only a fraction of the lycaenids. In addition, it is sometimes difficult to conclude from the literature records whether observed ant-associations are a regular phenomenon or only occur occasionally. Accordingly, species like *Lycaena dispar* or *Callophrys rubi* were repeatedly categorized as myrmecophilous on the grounds of single old records (e.g. Warnecke 1932/33, Hinton 1951, Kitching & Luke 1985), while more recent studies either did not mention myrmecophily as a significant factor (*L. dispar*: Duffy 1968), or even demonstrated that ant-associations are exceptional events at most (*C. rubi*: Fiedler 1990d).

Given the large species diversity of the Lycaenidae and the considerable difficulties associated with field studies on their larval ecology, thorough ecological investigations of a taxonomically representative number of species are beyond reach. Thus, future research must further largely pertain to the description of life-histories, while the

necessary detailed ecological and physiological studies will unevitably remain restricted to a small number of "model species".

Hence, comparative investigations using the myrmecophily parameters described above may turn out extremely useful, because they rather rapidly yield data on the extent of ant-associations in a number of species. For the progress in understanding the evolution of lycaenid-ant interactions, such a more complete comparative knowledge is crucial.

Using the myrmecophily parameters A, RV, and P the caterpillar species investigated are divided into four groups. *P. coridon* was highly myrmecophilous, *P. icarus* more weakly ant-associated (with all myrmecophilous organs less attractive and less active than in *P. coridon*), the *Lycaena* species were myrmecoxenous and only partially induced ant-associations, and *Callophrys rubi* as well as the riodinid *Hamearis lucina* were totally unattractive to ants and were sometimes even attacked. *P. escheri* (see above) and *P. daphnis* (Fiedler, unpublished) likewise belong to the distinctly ant-attractive species.

Malicky (1969b), in his extensive studies using a larger number of European lycaenid species, gave few quantitative details of his experiments. Nevertheless, it is possible to compare some of his results with this categorization. According to his Tab.5 (Malicky 1969b:261) the following species are highly attractive to ants:

The polyommatines *Celastrina argiolus, Scolitantides orion, Pseudophilotes schiffer-muelleri, Plebejus argus, P. (Lycaeides) idas, P. (L.) argyrognomon, Polyommatus (Aricia) agestis, P. (Agrodiaetus) damon, P. (Lysandra) dorylas, P. (Meleageria) daphnis*, and perhaps *Satyrium spini* (Eumaeiti). All these species possess a functional DNO and (with the exception of *S. spini*) a pair of TOs. *P. damon* and *P. dorylas* apparently everted their TOs less frequently than the remaining species, but for *P. dorylas*, at least, the alerting function of the TOs has been observed in the field (Munguira & Martín 1989b). Furthermore, all these species have well-known ant-associations in the field (see Appendix), although in *C. argiolus* ant-associations are seemingly not universal (Harvey & Webb 1980, Emmet & Heath 1990).

Judging from Malicky's data the following species belong to the second group with rather weak myrmecophily:

The Eumaeiti species *Satyrium w-album, S. ilicis*, and possibly *S. acaciae*, as well as *Polyommatus amandus* and *P. thersites*. All of them have well established ant-associations in the field and possess a functional DNO (see Appendix) with the exception of *S. acaciae*. The latter has apparently never been found with ants, and at another place Malicky (1969b:248) notes that the DNO of its larvae may be rudimentary.

The third group comprises the Theclini species *Thecla betulae* and *Quercusia quercus*, the *Lycaena* species *phlaeas, tityrus, virgaureae, dispar* and *hippothoe*, and the Eumaeiti species *Satyrium (Fixsenia) pruni*. Caterpillars of these species were sometimes found to be attractive and were in part intensively palpated, but all lack a functional DNO (Malicky states that *S. pruni* has a DNO, but SEM studies of Kitching & Luke [1985] proved this organ to be absent). Correspondingly, larvae of all these species have never or only very occasionally been found associated with ants in the field.

The totally unattractive species were the same as in my experiments, viz. *Callophrys rubi* (Malicky 1969b:278) and *Hamearis lucina* (loc. cit.:266).

Thus, despite the lack of quantitative data and the use of different ant species, the experimental results of Malicky (1969b) largely agree with the categorization obtained from my laboratory studies. In addition, these categorization corresponds astonishingly well to the field data available, giving further support to the applicability of the experimental method developed here.

A direct comparison with the results of Ballmer & Pratt (in press) is more difficult, mainly due to the different experimental procedure. Ballmer & Pratt confronted one caterpillar with five ants (*Formica pilicornis*) for 5 min and only recorded the permanence of ant-associations (defined as the percentage time a caterpillar had contact with ants).

Nevertheless, the Californian species investigated can be grouped into three categories. Highly myrmecophilous caterpillars are visited by ants more than 90 % of the experimental time (e.g. three *Lycaena* species, *Harkenclenus titus, Phaeostrymon alcestis*, 6 *Satyrium* species, and 13 of 22 Polyommatini), and most of these have been recorded with ants in the field.

Moderately to weakly attractive were some *Callophrys* species, *Satyrium fuliginosum, Fixsenia ontario*, and four Polyommatini species. Distinctly unattractive were eight myrmecoxenous *Lycaena* species, the Thecliti genera *Habrodais* and *Hypaurotis*, four Eumaeiti species, and two myrmecoxenous riodinids. In all, this grouping rather well parallels the occurrence of ant-association in the field, but the congruence is less perfect than in the species covered in the present study.

Most likely, this is due to limitations of the experimental design employed: the focus on the short-time aspects of caterpillar-ant interactions may well mask distinct differences in the attractiveness of the caterpillars. Of course, the interpretation of laboratory results must always be done with caution, but the evaluation of the results of Malicky, of Ballmer & Pratt, and of this study shows that meaningful conclusions can be drawn with regard to the presence and extent of ant-associations in the field.

LYCAENID SYSTEMATICS AND MYRMECOPHILY

The system of the Lycaenidae

Previous studies of myrmecophily in the Lycaenidae were either based on now outdated higher classifications of the family (Warnecke 1932/33, Malicky 1969b), or they decidedly rejected any possible relations between higher classification and evolution of ant-associations (e.g. Pierce & Elgar 1985, Pierce 1987). It is one central aim of this study to show that, using a modern approach to the higher classification of the family Lycaenidae, important correlations between myrmecophily and systematics become obvious.

In the following I will first give a brief account of the classification upon which this study is based. The second part of this chapter deals with the occurrence of ant-associations and myrmecophilous organs in the various subgroups of the Lycaenidae, and the third part gives a short characterization of all major lycaenid taxa with respect to myrmecophily.

The higher classification of the Lycaenidae is still far from being resolved in a thoroughly phylogenetic sense. Like in the second large butterfly family Nymphalidae (cf. Ackery 1988), a number of well defined and very probably monophyletic taxa exist in the Lycaenidae, but their exact relationships to each other are not yet sufficiently clear. The classical study of Eliot (1973) provides the basis for all modern approaches to Lycaenidae systematics. Scott & Wright (1990) rearranged and somewhat harmonized this classification, and I largely adopt this with only minor alterations (Tab.3).

According to this system the Lycaenidae consist of the 4 subfamilies Poritiinae, Miletinae, Curetinae, and Lycaeninae. The Riodinidae, often treated as a subfamily of the Lycaenidae (e.g. Scott 1985, Scott & Wright 1990), are here viewed as a distinct family. Harvey (1987) proposed the Riodinidae being the sister-group of the Lycaenidae, but according to Robbins (1988a) the Riodinidae may rather form a monophyletic unit together with the Nymphalidae.

Furthermore, the riodinids have followed an entirely convergent, but not homologous evolutionary pathway with respect to myrmecophily (DeVries 1990b). Therefore, the treatment of the riodinids as a distinct family avoids the possible paraphyly of the Lycaenidae s.l. (i.e. including the riodinids).

The remaining lycaenid subfamilies are still not of identical rank in a cladistic system, but a more sophisticated hierarchy must await further analysis. For a detailed account of all relevant morphological characters the reader is referred to Eliot (1973), Scott (1985), Harvey (1987), Robbins (1988a, b), and Scott & Wright (1990). Stempffer's (1967) and Eliot's (1973) treatises also encompass historical perspectives of lycaenid systematics. The present study is not intended to revise the classification of the Lycaenidae, and in the following I only briefly discuss those characters related to myrmecophily.

The Poritiinae and Miletinae lack a number of apomorphic characters of the Lycaeninae and are thus usually viewed as the earliest branches of the Lycaenidae. Several

Tab.3: The higher taxa of the Lycaenidae (modified from Scott & Wright 1990) with approximate species numbers (after Bridges 1988), numbers of species with life-history information available (percentage in brackets), and main area of distribution.
*: Larvae with only dorsal nectary organ (DNO) recorded;
+: larvae with DNO and tentacle organs (TOs);
T: only TOs present.

a) Lycaenid subfamilies, and Poritiinae and Miletinae tribes

Taxon	Species number	Life-history information	Main distribution
Poritiinae	572	59 (10.3)	Palaeotropical
Poritiini	52	1 (1.9)	Oriental
Liptenini	520	58 (11.2)	African
Miletinae	140	37 (26.4)	Palaeotropical
Miletini	120	28 (23.3)	Oriental
Liphyrini T	20	9 (45.0)	African
Curetinae T	18	6 (33.3)	Oriental
Lycaeninae +	3640	968 (26.6)	Cosmopolitan
Aphnaeini +	253	77 (30.4)	African
Lycaenini	92	38 (41.3)	Holarctic
Theclini +	530	120 (22.6)	Palaeotropical
Eumaeini +	1580	367 (23.2)	South Hemisphere
Polyommatini +	1182	366 (31.0)	Old World

b) Theclini subtribes

Taxon	Species number	Life-history information	Main distribution
Luciiti +	149	43 (28.9)	Australian
Ogyriti +	15	12 (80.0)	Australian
Zesiiti +	11	11 (100)	Australian
Arhopaliti +	236	20 (8.5)	Oriental
Thecliti (*)	119	34 (28.6)	Sino-Oriental

c) Eumaeini subtribes

Taxon	Species number	Life-history information	Main distribution
Catapaecilmatiti +	11	2 (18.2)	Oriental
Amblypodiiti +	13	8 (61.5)	Palaeotropical
Oxyliditi ?	8	0	African
Hypothecliti ?	3	0	Australian
Loxuriti +	57	11 (19.3)	Oriental
Iolaiti +	206	64 (31.1)	Palaeotropical
Remelaniti *	7	2 (28.6)	Oriental
Hypolycaeniti *	53	13 (24.5)	Palaeotropical
Deudorigiti +	200	46 (23.0)	Palaeotropical
Eumaeiti *	1023	221 (21.6)	Neotropical

d) Subtribes and sections of the Polyommatini

Taxon	Species number	Life-history information	Main distribution
Candaliditi +	30	14 (46.7)	Australian
Lycaenesthiti +	136	33 (24.3)	African
Niphanditi +	6	1 (16.7)	Oriental
Polyommatiti +	1010	318 (31.5)	Old World
Cupidopsis	3	2 (66.7)	African
Nacaduba	146	29 (19.9)	Oriental
Jamides	91	12 (13.2)	Oriental
Uranothauma	42	19 (45.2)	African
Leptotes	23	9 (39.1)	African
Castalius	37	21 (56.8)	Palaeotropical
Zizeeria	19	14 (73.7)	Palaeotropical
Everes	77	27 (35.1)	Old World
Lycaenopsis	113	15 (13.3)	Oriental
Glaucopsyche	53	33 (62.3)	Holarctic
Euchrysops	175	49 (28.0)	African
Polyommatus	231	88 (38.1)	Palaearctic

characters indicate that Poritiinae and Miletinae may be sister-groups (Scott & Wright 1990, Eliot, pers. comm.).

The Poritiinae consist of two tribes, the Oriental Poritiini (> 50 spp.; all species numbers are approximate figures based on the catalogue of Bridges 1988) and the African Liptenini (>520 spp.). The Liptenini are further subdivided into three subtribes (Pentiliti, Durbaniiti and Lipteniti).

The largely Palaeotropical Miletinae, as well, comprise two tribes, the Miletini (120 spp., including the subtribes Spalgiti, Tarakiti, Miletiti and Lachnocnemiti) and the mainly African Liphyrini (20 spp.). Eliot (pers. comm.), however, relates the Lachnocnemiti with the Liphyrini.

The systematic position of the third Oriental subfamily Curetinae (18 spp.) is still uncertain. Previously sometimes even treated as a distinct family (Shirôzu & Yamamoto 1957), the Curetinae have later been placed at various positions within the Lycaenidae. Scott (1985) suggested the Curetinae to be the sister-group of the Riodinidae, whereas Scott & Wright (1990) claim a sister-group relationship with the Lycaeninae. Robbins (1988a), however, provided evidence that the Curetinae might form a monophyletic unit together with the Poritiinae and Miletinae, and Eliot (pers. comm.) supports this latter view. Anyway, the Curetinae (consisting only of the genus *Curetis*) possess a number of highly apomorphic characters together with some primitive features which makes a final decision yet impossible.

The last and by far most species-rich subfamily are the Lycaeninae (3640 spp.). They have a worldwide distribution and are further subdivided into 5 tribes. Only three of these are well defined monophyletic taxa: Aphnaeini, Lycaenini, and Polyommatini.

The Lycaenini comprise less than 100 predominantly Holarctic species, and the largely African Aphnaeini contain about 250 species.

The monophyly of the third tribe Theclini (c. 530 spp.) is questionable. Previous classifications (e.g. Eliot 1973) used the name "Theclinae" in an even much broader sense, but this assemblage appears to be paraphyletic (Scott & Wright 1990). The Theclini, as defined by Scott & Wright (1990), are grouped into five subtribes with characteristic distributional patterns (Tab.3): Luciiti, Ogyriti, Zesiiti, Arhopaliti, and Thecliti.

The phylogenetic relationships among these subtribes are unclear. Luciiti, Ogyriti and Zesiiti are rather isolated and presumably old, mainly Australian lineages, wheras Arhopaliti and Thecliti together possibly constitute a monophyletic unit (Eliot, pers. comm.), the Thecliti being the temperate Asian equivalent to the tropical Oriental Arhopaliti.

The fourth and most diverse tribe are the Eumaeini (c. 1580 species). The systematics of this group as well as its monophyly are poorly documented. The Eumaeini roughly fall into two groups: a number of subtribes in the Old World, and the largely Neotropical Eumaeiti ($>$ 1000 species).

The latter are monophyletic and are represented in the northern hemisphere with only about 60 species each in the Nearctic and Palaearctic region, respectively. More than 900 Eumaeiti species are strictly Neotropical, and their systematics and ecology are in urgent need of further work (Robbins, pers. comm.). The Old World Eumaeini subtribes are split into a number of taxa according to Eliot (1973) and Scott & Wright (1990). However, Eliot himself (in Corbet & Pendlebury 1978) has questioned the validity of several of these separations.

For the purpose of this study I here lump together some of these, using suggestions of Eliot (pers. comm.). Accordingly, the Old World Eumaeini consist of the subtribes Catapaecilmatiti, Amblypodiiti, Oxyliditi, Hypothecliti (perhaps better placed in the Theclini?, Eliot, pers. comm.), Loxuriti (including the Cheritriti and Horagiti sensu Scott & Wright 1990; see Corbet & Pendlebury 1978), Iolaiti, Remelaniti, Hypolycaeniti, and Deudorigiti (including Tomariti). There is some evidence that Deudorigiti and Eumaeiti are sister-groups, but the phylogenetic relationships of the remaining subtribes to each other are unknown.

I have largely adopted this subdivision simply in the absence of better alternatives, and further research may well reveal that the Eumaeini subdivision adopted here goes too far. Also, some of the taxa included may turn out to be more closely related to what is here termed "Theclini".

The last tribe of the subfamily Lycaeninae are the Polyommatini ($>$ 1180 species). They are very probably monophyletic and can further be subdivided into four subtribes (Candaliditi, Lycaenesthiti, Niphanditi, and Polyommatiti). The Polyommatiti are by far the largest of these ($>$ 1000 species) and were grouped in a number of sections by Eliot (1973). Again Eliot's subdivision created a number of very small taxa of somewhat

questionable significance, and I have tentatively grouped those together where a clear relationship was indicated by Eliot (1973).

The following sections are recognized within the Polyommatiti: *Cupidopsis* section, *Nacaduba* section (including the *Petrelaea, Theclinesthes, Upolampes* and *Danis* sections of Eliot), *Jamides* section (including *Catochrysops* and *Lampides* sections), *Uranothauma* section (including *Phlyaria* and *Cacyreus* sections), *Leptotes* section, *Castalius* section, *Zizeeria* section (including *Zintha, Famegana, Actizera, Zizula* and *Brephidium* sections), *Cupido* section (including *Pithecops, Azanus* and *Eicochrysops* sections), *Lycaenopsis* section, *Glaucopsyche* section, *Euchrysops* section, and *Polyommatus* section (see Tab.3).

Tab.3 summarizes this systematic approach. It must be emphasized again that the higher classification of the Lycaenidae as suggested here is not yet a truly phylogenetic one. However, this classification likely parallels the phylogeny of the Lycaenidae more closely than all pre-Eliotian attempts.

As will be seen later, this classification, albeit mainly based on adult morphological characters, is in surprisingly good agreement with the zoogeography of the lycaenid subgroups and the information available on morphology and biology of the early stages. It seems thus feasible to base the discussions of lycaenid myrmecophily on this approach, but one should always keep in mind that future research on the cladistics of the Lycaenidae will certainly lead to a number of improvements and changes.

Systematic distribution of myrmecophilous organs within the Lycaenidae

Most approaches to the higher classification of the Lycaenidae, including Scott & Wright (1990), assume that myrmecophily is an ancestral character of the family. As a logical consequence, all cases where neither myrmecophilous organs nor ant-associations are present must be viewed as secondary losses in such scenarios. In other words: myrmecoxeny within the Lycaenidae would always be a secondary trait.

This paragraph is devoted to the question which lycaenid taxa possess what types of myrmecophilous organs and ant-associations. As a result the hypothesis of ancestral myrmecophily and the systematic position of some lycaenid taxa will be critically re-examined.

The outgroups: Nymphalidae and Riodinidae

Any interpretation of a character state as plesiomorphic or apomorphic in a phylogenetic context must imply the outgroup comparison as most important methodology (Hennig 1982, Ax 1984). Irrespective of the detailed position of the Riodinidae, most modern authors (e.g. Kristensen 1976, Scott & Wright 1990) agree that Lycaenidae, Riodinidae and Nymphalidae together constitute a monophyletic taxon. Likewise, there is broad agreement that the Nymphalidae are monophyletic.

Thus there are two outgroups that should be considered with respect to the ancestral Lycaenidae, viz. the Nymphalidae and the Riodinidae. In the large family Nymphalidae

no single case of larval myrmecophily is known, nor does any known nymphalid larva possess any myrmecophilous organs. Unless one assumes that the ancestor of all Nymphalidae has lost its myrmecophily, the unavoidable and most parsimonious interpretation is that the ancestor of the nymphalids as well as that of the whole group Nymphalidae + Riodinidae + Lycaenidae was primarily myrmecoxenous, as are all other Papilionoidea.

Within the Riodinidae myrmecophilous organs and ant-associations are known or suspected from quite a number of species. However, the larval myrmecophilous organs of the Riodinidae are structurally and functionally different from those of the Lycaenidae and occur in different locations (Ross 1964, Cottrell 1984, DeVries 1988, 1990). They are hence viewed by DeVries (1990b) as analogous, but not homologous structures of the caterpillars. In addition, myrmecophily within the Riodinidae is confined to the tribes Eurybiini, Lemoniini and Nymphidiini of the subfamily Riodininae. These tribes are considered as the most advanced of the whole family, representing less than an estimated 300 species (Harvey 1987).

Accordingly, myrmecophily and the possession of ant-organs are viewed as an apomorphic character state of these three tribes, whereas taxonomic groups such as Hamearinae, Euselasiinae, and five Riodininae tribes entirely lack ant-associations and myrmecophilous organs. The latter taxa share a number of other independent plesiomorphic traits and are thus believed to have split off from the stem group of the higher Riodininae prior to the evolution of myrmecophily (Harvey 1987). This taxonomic distribution of ant-associations provides strong evidence that the ancestral Riodinidae were primarily myrmecoxenous.

With respect to the presumed sister-group relationship between Riodinidae and Lycaenidae this conclusion implies that a number of characters related to myrmecophily are not synapomorphies of the Lycaenidae + Riodinidae as a whole. Examples taken from Scott & Wright (1990) are: the thick larval cuticle (which is not typical for riodinid caterpillars); the ability to retract the head beneath the prothorax (typical for Lycaeninae larvae, but only weakly developed in the Riodinidae and in several lycaenid lineages); the tentacle organs on the eighth abdominal segment (missing in all primarily myrmecoxenous riodinids, structurally and functionally different in myrmecophilous riodinids); the dorsal nectary organ (totally absent in all riodinids); and the preference of the larvae for young plant tissue, flowers or fruits (riodinids generally feed on mature leaves, only myrmecophilous species tend to prefer plants bearing extrafloral nectaries and even utilze this nectar: Harvey 1987, DeVries 1990b, DeVries & Baker 1990).

The only type of larval organs related to myrmecophily that is common to both Riodinidae and Lycaenidae are the pore cupola organs (PCOs) or "lenticles". However, as already explained in the introduction, the PCOs of riodinids, including myrmecophilous species, are not attractive to ants (DeVries 1988, Harvey 1989). Therefore, even if the PCOs are a synapomorphy of Riodinidae and Lycaenidae (Harvey 1987), their connection to myrmecophily is almost certainly restricted to the Lycaenidae s. str. (experimental evidence for the ant-attractiveness of the PCOs is even restricted to the subfamily Lycaeninae). The ancestral function of the PCOs remains unknown.

Summarizing the above arguments, the outgroup comparisons with the Nymphalidae and Riodinidae lend no support to the idea that these two taxa were primarily myrmecophilous, irrespective of their detailed phylogenetic relationships to the Lycaenidae.

The subfamilies Poritiinae, Miletinae, and Curetinae

It is generally accepted that Poritiinae and Miletinae are the earliest offshoots form the common ancestral Lycaenidae stem. The presence of PCOs in the Poritiinae is very likely (see Clark & Dickson 1971), but requires confirmation. There is no indication that any Poritiinae larva hitherto known possesses either a DNO or a pair of TOs. Instead, Poritiinae caterpillars are usually hairy (at least in later instars), and in the Riodinidae hairiness is markedly correlated with myrmecoxeny (DeVries 1990b).

Larvae and pupae of the Miletinae (except the highly specialized *Liphyra brassolis*) possess PCOs, although their morphology differs from the types found in the Lycaeninae and some Riodinidae (Kitching 1987; Fiedler, unpublished). A DNO has not been observed in the Miletinae, but Kitching (1987) mentions a structure on the seventh abdominal segment of *Allotinus major* that he calls "pseudo-Newcomer's organ". However, the glandular nature of this structure has not been proved, and many Miletinae caterpillars are not attractive for ants, but are either sometimes attacked (*Feniseca, Spalgis?*) or largely ignored by ants (see below).

TOs on the eighth abdominal segment are only known from one African Liphyrini genus, *Aslauga* (Jackson 1937, Boulard 1968, Cottrell 1981, 1984, Villet 1986). Lamborn (1914) observed that these TOs "are thrust out from time to time", but he did not mention any relation to the presence of ants.

In summary, the larvae of both, the Poritiinae and Miletinae, lack the typical myrmecophilous organs of higher lycaenids except the seemingly ubiquitous PCOs. The isolated occurrence of TOs of unknown function in one single genus (*Aslauga*) is indicative of an independent evolution of this character rather than of an ancestral equipment with TOs that were subsequently lost in all Poritiinae and the vast majority of the Miletinae (Eliot, pers. comm.).

The placement of the Curetinae is still discussed controversially (see above). Anyway, whether they are interpreted as the sister-group of the Lycaeninae (Scott & Wright 1990), as a part of a taxon comprising Poritiinae, Miletinae and Curetinae (Robbins 1988a), or even as the earliest offshoot of the Lycaenidae as a whole (Eliot, pers. comm.), all these interpretations view this subfamily as ancestral in relation to the Lyaeninae.

Larvae and pupae of its only genus *Curetis* possess strikingly aberrant epidermal organs. The functions of these organs (e.g. "perforated chambers": DeVries et al. 1986) remain unknown. PCOs are present, but their structure is unique in the larvae (DeVries et al. 1986), and the pupal PCOs can only be recognized as such on the grounds of their locations (Fiedler, unpublished). A DNO is not known from *Curetis* larvae. Instead they possess a specialized groove of unknown function between the abdominal segments 7 and 8 (DeVries et al. 1986). As with the "pseudo-Newcomer's organ" of *Allotinus* it is

unclear and rather unlikely whether this organ of *Curetis* is homologous to the true DNO of the Lycaeninae (Scott & Wright 1990, Eliot, pers. comm.).

TOs are well developed and very large in the Curetinae, but, as already noted by Viehmeyer (1910a), their homology to the TOs of the Lycaeninae seems questionable. They are different not only in function (*Curetis* larvae evert their TOs in response to tactile disturbance and hereby try to ward off potential enemies: Fiedler & Maschwitz, unpublished), but also in location (medioposterior of the spiracle in Curetinae, lateroposterior of the spiracle in Lycaeninae). Thus, the TOs of *Curetis* are most likely the result of convergent evolution (Eliot, pers. comm.), as it is the case with the TOs of Riodinidae (DeVries 1990) and, probably, *Aslauga* (see above).

Looking now back on the 3 lycaenid subfamilies Poritiinae, Miletinae, and Curetinae, the following generalizations are possible:

1.) PCOs are widespread, if not ubiquitous, but, as in the Riodinidae, there is no evidence that these organs are attractive to ants.

2.) A DNO is always absent. There is no plausible morphological or functional indication for a homology between the epidermal grooves of *Allotinus* and *Curetis* and the true DNO of the Lycaeninae.

3.) TOs are present only in two isolated genera (*Curetis, Aslauga*), and it is very likely that these structures evolved independently of the TOs of the Lycaeninae. The general potential to develop eversible epidermal structures is obviously an ancestral character of the whole Riodinidae-Lycaenidae group.

Thus, neither the comparative study of the larval and pupal morphology of the Lycaenidae subfamilies retaining a number of plesiomorphic characters, nor the comparisons with Nymphalidae and Riodinidae as outgroups lend support to the idea of ancestral myrmecophily. Instead, the ancestral lycaenids apparently had primarily myrmecoxenous caterpillars, and only a small fraction of them evolved myrmecophilous life-habits as carnivorous or ant-parasitic species (Miletinae), or perhaps as commensales (Poritiinae, see below). The "typical" myrmecophily of lycaenid caterpillars is restricted to the largest subfamily Lycaeninae.

Myrmecophilous organs of the Lycaeninae

The larvae within this subfamily primarily bear a full set of ant-organs (PCOs, a DNO and TOs), and they are generally myrmecophilous. In fact, the true DNO is confined to this subfamily and represents one of its most important synapomorphies.

The Aphnaeini are now generally accepted as the earliest offshoot from the Lycaeninae, and in nearly all known Aphnaeini larvae this equipment has been retained. Only in some species of *Aloeides* and in the small genus *Phasis* the DNO is reduced, at least in the final instar (Clark & Dickson 1971, Henning 1983a). On the other hand, some species (*Spindasis, Crudaria leroma*) possess further, presumably glandular structures ("dish organs": Clark & Dickson 1971, Cottrell 1984) that are highly attractive to ants. The TOs of the specialized "whip type" are always well developed from the first instar on (Clark & Dickson 1956).

Caterpillars of the tribe Lycaenini all lack the DNO and TOs, but possess PCOs. Many Lycaenini pupae and the larvae of at least four North American *Lycaena* species additionally possess dendritic setae that seem to be related to myrmecophily (Ballmer & Pratt 1988 and in press). Typically, Lycaenini larvae are myrmecoxenous, this trait most likely being a case of secondary reduction.

It is, however, not yet clear from which lycaenid group this reduction had started. Three hypotheses exist that are all supported by some evidence.

— The Lycaenini may have branched off from the Lycaeninae stem as the second group after the Aphnaeini (this possibility is in accordance with the similarities between Aphnaeini and Lycaenini in external appearance as well as with the apparent early origin of the Lycaenini as indicated by their zoogeography).

— Or the Lycaenini may be the sister-group to, or even a specialized, but early offshoot from the Polyommatini (Eliot, pers. comm.).

— Or the Lycaenini may be the sister-group of the Eumaeini + Polyommatini (based on some characters of first instar larvae: Scott & Wright 1990).

Irrespective of the detailed phylogeny of this tribe, it is important to note that myrmecoxeny is probably a secondary character of Lycaenini larvae, whereas in the Riodinidae subfamilies Hamearinae and Euselasiinae, and the lycaenid subfamilies Poritiinae, Miletinae, and Curetinae, myrmecoxeny is a primary character state. Alternatively, one would have to assume that the Lycaenini are the sister-group of the remaining Lycaeninae tribes, or that the DNO of Aphnaeini and of the tribes Theclini, Eumaeini and Polyommatini have evolved in parallel. For both these ideas there is at present no support.

The majority of Theclini larvae possess the full complement of myrmecophilous organs. The TOs of Theclini, Eumaeini and Polyommatini, however, are always smaller than those of the Aphnaeini ("beacon type" of Clark & Dickson 1956). Reductions repeatedly occur in several groups.

At least some species of the Luciiti genus *Philiris* have neither a DNO nor TOs (Ballmer & Pratt 1988), while others have apparently retained the DNO at least (Parsons 1984). The TOs are likewise lost in the genus *Acrodipsas* whose larvae permanently live inside ant-nests (Samson 1989).

The second Theclini subtribe with reduced myrmecophilous organs are the Thecliti. In this group the TOs are entirely missing, and the presence of the DNO has not yet been confirmed without doubt (e.g. Malicky 1969b). The only Thecliti species with all ant-organs present is the systematically isolated *Amblopala avidiena* (Uchida 1985).

Eumaeini larvae are basically myrmecophilous, as well, and they bear all types of ant-organs. This situation is largely retained in the subtribes Catapaecilmatiti, Amblypodiiti and Loxuriti. However, reductions of the myrmecophilous organs and secondary myrmecoxeny are widespread among the Eumaeini.

In the subtribe Iolaiti records of ant-associations are scattered. At least some Iolaiti species are suspected to have a reduced set of ant-organs (Farquharson 1922; but see Clark & Dickson 1971). In the Deudorigiti, certain endophytic species have lost the

TOs, and some have even reduced the DNO. The most pronounced tendency to reduce ant-associations is found in the Eumaeiti. No Eumaeiti larva is known to possess TOs, and the DNO is sometimes reduced to a non-functional rudiment (e.g. some *Callophrys* and *Satyrium* species: Malicky 1969b, Fiedler 1990d), or even completely lost in a number of species (e.g. *Eumaeus* spp., *Satyrium pruni, Erora* spp., see Appendix).

Polyommatini caterpillars usually possess all types of myrmecophilous organs and are associated with ants. Reductions of the TOs occur in several endophytic genera (*Cacyreus, Harpendyreus, Cupido*) and in those species living inside ant-nests (*Maculinea, Lepidochrysops*), while total reductions of both DNO and TOs are rare (*Cacyreus, Udara blackburni, Plebejus optilete*, subgenus *Agriades* of *Polyommatus*; see Appendix).

The higher lycaenid taxa and their ant-associations

Poritiinae

The only Poritiini species whose larval biology is known (*Poritia erycinoides*) has hairy caterpillars that live gregariously on Fagaceae trees without being ant-attended (Rosier 1951).

Liptenini larvae are extremely hairy as well, but feed on lichen and similar substrates. Ant-associations are entirely unknown from Pentiliti and Durbaniiti, while the larvae of some Lipteniti genera (*Liptena, Teratoneura, Deloneura, Epitola, Hewitsonia*) appear to be mostly found on trees occupied by *Crematogaster* ants (Farquharson 1922, Jackson 1937, Ackery & Rajan 1990). However, direct caterpillar-ant interactions have rarely been reported, and Farquharson (1922) observed that the ants always avoided contacts with the fuzzy caterpillars of *Teratoneura isabellae*. Thus, the relationship between these Lipteniti larvae and ants is co-existence (or perhaps commensalism in a few cases) rather than myrmecophily in a more sophisticated sense.

Anyway, the Poritiinae are one of the lycaenid groups where the knowledge of larval biology is distinctly insufficient, and the description of further life-histories almost certainly will modify the current picture.

Miletinae

Miletinae larvae are carnivorous or feed on excretions of Homoptera or trophallactic regurgitations of ants (Cottrell 1984).

Within the Miletini, caterpillars of the least specialized subtribes Spalgiti and Tarakiti (*Spalgis, Feniseca, Taraka*) feed on ant-tended coccids, but are not always tolerated by the ants. As protective device they either feed inside silken shelters (*Feniseca, Taraka*), or they cover themselves with the remains of their prey (*Spalgis*). Thus, Spalgiti and Tarakiti larvae are not truly myrmecophilous. The caterpillars of the Miletiti, in contrast, are usually fully tolerated, but largely ignored within the trophobiotic ant-Homoptera associations (*Logania, Allotinus, Miletus, Megalopalpus*).

At least some Miletiti species have in fact close relationships to ants, either using ants as oviposition cues (*Allotinus unicolor, Miletus* spp.: Maschwitz et al. 1988, Fiedler & Maschwitz 1989c) or even living and pupating inside ant nests (*Allotinus apries, Miletus* spp.: Cottrell 1984, Maschwitz et al. 1988).

Even closer ant-associations occur in the Lachnocnemiti. *Lachnocnema bibulus* larvae have been observed to be carried into *Camponotus* nests (Cripps & Jackson 1940), and the caterpillars of at least some *Thestor* species live and pupate inside *Anoplolepis* nests (Clark & Dickson 1971).

The second Miletinae tribe Liphyrini, then, is highly adapted to live in association with ants. *Aslauga* larvae feed on Homoptera and are ignored by ants (as with *Allotinus*), while *Liphyra* and *Euliphyra* are specialized predators or parasites in *Oecophylla* nests.

In all, Miletinae caterpillars are well adapted to avoid ant-attacks when preying upon the ants' trophobionts, but true myrmecophily has been evolved independently only in some advanced groups, and all these myrmecophiles are detrimental to their ant hosts. The systematic distribution of myrmecophily within the Miletinae indicates an evolutionary sequence from loose and incidental associations, over consistently tolerated "guests" in trophobiotic associations, up to highly adapted inquilines.

Curetinae

Curetis larvae are usually not ant-associated (Hinton 1951, Iwase 1954, Eliot 1980). DeVries (1984) found larvae of *C. regula* visited by ants (*Anoplolepis longipes*), but these ants were mostly attracted to the sap-flow caused by the larval feeding activities and largely ignored the caterpillars themselves.

Own observations with *C. felderi* revealed that the larvae are not attractive to ants (*Anoplolepis, Oecophylla, Pheidole*) and, in particular, do not release the typical palpation behaviour. One *Crematogaster* species even severely attacked a caterpillar. When observed on the natural hostplant without disturbance, *C. felderi* larvae were ignored by *A. longipes* that attended the extrafloral nectaries of the hostplant. The TOs were never seen everted unless a caterpillar was prodded (using a blade of grass), or was attacked by *Crematogaster* ants. The latter were not repelled by repeated TO eversions (Fiedler & Maschwitz, unpublished). In summary, the current evidence indicates that Curetinae larvae are not really myrmecophilous.

Lycaeninae

A p h n a e i n i — All species of this tribe, for which sufficient life-history information is present, are at least facultatively associated with ants. In the majority of cases their myrmecophilous relationships appear to be even obligatory and specific.

Larvae of the genera *Aphnaeus, Spindasis, Cigaritis, Crudaria, Phasis, Aloeides* and *Poecilmitis* often rest or diapause in ant nests, and their host ants are in constant attendance. Some caterpillars are known or strongly suspected to be fed by ant-regurgitations (*Spindasis, Cigaritis, Axiocerses*).

In other species the females only oviposit in the presence of the appropriate host ants (e.g. Henning 1983a, b). The myrmicine ant genus *Crematogaster* is the dominant host taxon for Aphnaeini caterpillars, but a few of them have other host ants (*Aloeides, Erikssonia: Acantholepis; Poecilmitis pyroeis: Camponotus*).

Some species in the genera *Spindasis* and *Cigaritis* apparently are commensales in ant nests (Hinton 1951, Larsen & Pittaway 1982), and the larvae of the genera *Tylopaedia, Trimenia, Argyrocupha*, and *Oxychaeta* are strongly suspected to be entirely aphytophagous, probably living as brood predators inside ant nests (Clark & Dickson 1971, Cottrell 1984).

As a whole, the Aphnaeini are the lycaenid tribe with the most intimate and specific relationships towards ants, and no single case of secondary myrmecoxeny is known from that group.

L y c a e n i n i — Ant-associations are rare in this tribe, suggesting that the larvae of the copper butterflies are usually myrmecoxenous. Their PCOs are attractive to ants, but this attractiveness is normally not sufficient to induce stable ant-associations (see above).

Old records of ant-associations are available for the Palaearctic *Lycaena dispar* (Hinton 1951), but require confirmation, since in the extensive recent literature about this locally endangered species no such associations are mentioned (e.g. Duffy 1968, but see Ebert & Rennwald 1991).

The four North American species with myrmecophilous larvae bearing dendritic setae (*Lycaena rubidus, xanthoides, editha* and *heteronea*) have already been mentioned (Ballmer & Pratt 1988, and in press). The presence of dendritic setae in the larvae of these four species must be regarded as an apomorphic character state, and thus their ant-associations may represent a kind of "tertiary myrmecophily" within the Lycaenini. Females of *L. rubidus* have been observed to oviposit in association with *Formica* ants (Funk 1975, Pierce, pers. comm.), and a closer investigation of this phenomenon seems worthwhile.

T h e c l i n i — Judging from the widespread records of ant-associations, Theclini caterpillars are generally myrmecophilous, although information regarding the two most species-rich subtribes Luciiti and Arhopaliti is still very scanty.

A number of Luciiti species (*Lucia, Paralucia*, and partly *Hypochrysops*) are obligatorily associated with specific host ants (Common & Waterhouse 1981, Sands 1986), and the *Acrodipsas* species even live as brood predators inside ant nests throughout their whole larval period (Samson 1989). Reductions of myrmecophily occur in the genus *Philiris* (Parsons 1984, Wood 1984).

The Ogyriti, Zesiiti and Arhopaliti are entirely myrmecophilous, as far as is known to-day, again with numerous obligatory ant-caterpillar relationships.

The Thecliti larvae, however, with their ant-organs reduced (see above), largely lack ant-associations (Iwase 1954, Shirôzu 1962). The only well documented myrmecophile in this subtribe is *Shirozua jonasi* whose larvae feed on aphids, their honeydew, and

regurgitations of the specific host ant *Lasius spathepus* (Cottrell 1984). In general, the Theclini can be described as a distinctly myrmecophilous taxon with reductions restricted to only two lineages.

E u m a e i n i — Ant-associations are widely distributed among this tribe, but reductions of ant-organs and myrmecophily are common in several of its subgroups.

The larvae of the subtribes Catapaecilmatiti, Amblypodiiti, Loxuriti and Iolaiti are generally myrmecophilous, but secondary myrmecoxeny is known from *Cheritra freija*. Judging from the scanty records the level of myrmecophily is generally low within the Iolaiti. No ant-associations have hitherto been reported for *Amblypodia anita* and numerous Iolaiti species, despite the presence of a DNO and TOs in most of them.

The Remelaniti and Hypolycaeniti are myrmecophilous, but TOs are only doubtfully recorded for *Ancema blanka* and two species of *Hypolycaena* (*H. lebona, H. othona*). TOs may in fact be missing in both groups. Two other species (*H. erylus, H. phorbas*) are the only well-documented examples of obligatory myrmecophily in the entire tribe Eumaeini with its more than 1500 species. Nothing is known about ant-associations in the subtribes Hypothecliti and Oxyliditi.

Myrmecophily has been reported from numerous Deudorigiti species, but reductions of ant-organs are not rare, especially among the species with larvae boring in flowers or fruits, where ants have limited access. The TOs, in particular, are missing in most species of the genus *Deudorix* s. l. and in *Capys*, whereas the genera *Rapala* and *Tomares* have retained their full complement of ant-organs and are facultatively myrmecophilous.

The largest subtribe Eumaeiti, which is undoubtedly closely related to the Deudorigiti, exhibits even more pronounced tendencies towards reductions of myrmecophily which closely parallel the reductions of ant-organs within this group (see above). None of the more than 1000 Eumaeiti species is yet known to be obligatorily myrmecophilous, and ant-associations have been definitely reported for only 27 of the 221 species where life-history information is available. As in the Deudorigiti, many species have endophytic fruit-boring larvae.

P o l y o m m a t i n i — Myrmecophily occurs nearly universally among Polyommatini caterpillars with only very few secondary exceptions. In the subtribe Candaliditi one species is stated to be myrmecoxenous (*Candalides albosericea*: Common & Waterhouse 1981), but no ecological and morphological details are given there.

The Lycaenesthiti are likewise ant-associated, and some species are known to be even obligate myrmecophiles. Two species were reported by Jackson (1937) to be myrmecoxenous, but this statement should be taken with caution on the following reasoning. Jackson, whose life-history reports are extremely accurate in other respects, stated that he could not find myrmecophilous organs on the larvae of four *Iolaus* and three *Anthene* species, but the painstaking studies by Clark & Dickson (1971) and Henning (e.g. 1983a) clearly confirmed the presence of all ant-organs in several closely related species.

Obviously, Jackson's optical equipment precluded a final decision in such species where the ant-organs are small or only occasionally extruded.

The life-history of only one species of the small subtribe Niphanditi has been recorded, this caterpillar being an obligate myrmecophile of *Camponotus* ants.

Well documented cases of secondary myrmecoxeny occur scatteredly in the Polyommatiti (*Uranothauma, Cacyreus, Udara blackburni, Plebejus optilete*, subgenus *Agriades* within *Polyommatus*). These are, however, rare exceptions that are by far outnumbered by the numerous obligatory ant-associations in the genera *Maculinea, Lepidochrysops*, and possibly *Tarucus* and *Plebejus*.

Viewing now back on the Lycaenidae as a whole, it becomes apparent that trophobiotic caterpillar-ant interactions are restricted to the subfamily Lycaeninae, due to the possession of the DNO as a keystone synapomorphy. However, within this subfamily myrmecophily is widespread and prevalent, the associations covering the entire range of ant-caterpillar interactions, from facultative or obligate trophobiosis to predatory parasitism, possibly commensalism, and simple coexistence.

The Lycaeninae tribes and subtribes usually exhibit characteristic levels of myrmecophily. Very close and often obligate ant-associations have mainly evolved in the Aphnaeini, Theclini, and in some Polyommatini. On the other hand, reductions of ant-organs and ant-associations have occurred in all tribes except the Aphnaeini, but secondary myrmecoxeny is typical only for the Lycaenini and Thecliti, and is rather widespread among the Deudorigiti and Eumaeiti.

The preceding two paragraphs gave a very condensed survey over the morphology and ecology of lycaenid caterpillars with respect to myrmecophily. Many details and references compiled in the tables (see Appendix) were omitted here, and all discussions were restricted to subfamilies, tribes, and subtribes.

Anyway, a generalized pattern becomes apparent, i.e. the major subtaxa of the family Lycaenidae have characteristic equipments with ant-organs as well as characteristic states of myrmecophily. This general pattern continues on the level of genus-groups ("sections") and genera, indicating that the evolution of myrmecophily is intimately correlated with the phylogeny of the lycaenid lineages.

In fact, on the grounds of this reasoning, any discussions on the evolutionary biology of lycaenid myrmecophily have to take into account such phyletic characteristics and trends. For example: a lycaenid group whose *Bauplan* does not include a DNO (e.g. Poritiinae, Miletinae) can never contain a species maintaining a trophobiotic relationship towards ants as so many Lycaeninae species do, unless within that group a convergent evolution of a trophobiotic gland would take place (as is the case with the myrmecophilous Riodininae tribes).

This conclusion is in marked contrast to the view of Pierce & Elgar (1985) and Pierce (1987: p.107) who stated that "the distribution of ant association within the Lycaenidae is independent of phylogeny". In fact it appears that myrmecophily remains a rather stable character in many lycaenid lineages.

This contrasts well with the trophobiotic associations of Homoptera and ants, that are often compared with lycaenid myrmecophily. In aphids, symbioses with ants have evolved several times in parallel, and ant-association is an evolutionarily rather labile trait (Bristow 1990). However, ant-homopteran mutualisms are based on excretions of superfluous carbohydrates, and these excretions provide a permanently available raw material for the evolution of complex interactions.

In lycaenid caterpillars, specialized glands are required that, once being evolved, were rather firmly incorporated into the morphological groundplan of their caterpillars. Accordingly, as already emphasized by Pierce (1987), ecological or evolutionary comparisons of interactions between ants and caterpillars or homopterans should always bear in mind the principal peculiarities of, and differences between, these organisms.

The pattern outlined here is far from being complete. Continuous recording of life-history information is necessary, especially in those groups where the knowledge is still very fragmentary (Poritiinae, Eumaeiti). Progress in the phylogenetic systematics of the Lycaenidae and their outgroups, as well, will certainly bring about new aspects and facets.

Nevertheless, based on this newly recognized systematic pattern and the life-history information compiled in the Appendix, it seems justified to critically re-examine some hypotheses concerning the specificity of lycaenid-ant interactions, the relations between hostplant choice and myrmecophily, and the biogeography of lycaenid myrmecophily in the following three main chapters. The final section will then consider some aspects of the evolutionary processes leading to, and modifying the ant-associations of the Lycaenidae.

SPECIFICITY OF LYCAENID-ANT INTERACTIONS

Which ants do visit lycaenid caterpillars?

Two general trends are found among the large number of myrmecophiles within the Arthropoda: ant species forming large and long-lived colonies are the preferred hosts of myrmecophiles, and most myrmecophiles are host-specific, i.e. they are associated with one ant species or genus only, or with a small group of ant host taxa (see Kistner 1982 and Hölldobler & Wilson 1990 for extensive reviews).

Both trends are easily understood: large ant colonies provide a significant and sufficiently stable resource in terms of food or shelter; and since ants are usually aggressive against any foreign intruders, specific mechanisms are required to overcome this aggressiveness and successfully enter into an ant society.

The majority of myrmecophiles, however, live inside ant nests at least during one part of their life-cycle and thus differ from the Lycaenidae, where most ant-associations occur outside ant nests on the appropriate larval hostplants. Ant-associations of lycaenid caterpillars in this respect largely parallel the myrmecophily of homopterans, and most trophobiotic associations of ants and homopterans are believed to be facultative or at least unspecific. There is, however, a growing body of evidence that homopterans may gain differential benefits from being attended by specific ants (Bristow 1984).

In addition, amazing specializations of trophobiotic systems have been discovered (e.g. Maschwitz & Hänel 1985). It is hence an interesting question whether the above rules regarding myrmecophily apply to the lycaenids as well.

The problem of specificity of lycaenid-ant interactions has previously been discussed by three authorities. Malicky (1969b), on the grounds of his extensive experimental work and compilation of literature data, concluded that most instances of lycaenid myrmecophily are rather unspecific. He found that most ants responded in largely the same way to a variety of lycaenid caterpillars tested by him. Only ants with special feeding habits (strictly predatory species, seed harvesters, social parasites) never formed associations with larvae.

According to Malicky, the main factor deciding which ants attend which lycaenids in nature is the structure of the ant fauna in the respective microhabitat. Hence, lycaenid larvae living in a given stratum are visited by ants sharing the same niche, and dominant ant species are more likely to be found attending caterpillars than subdominant ant species.

As a consequence, Malicky (1969b) suggested that most cases of lycaenid myrmecophily are unspecific and facultative. Specific relationships were only accepted by him for parasitic species such as *Maculinea*, and he also suspected that among the tropical lycaenids a further number of specific and obligate ant-associations should occur. At that time the knowledge of most tropical taxa was too scanty to allow a more precise assessment.

Cottrell (1984), in his extraordinarily complete review paper, broadly followed this argumentation. However, having compiled data for a larger number of tropical species, he concluded that specific associations occur not only with most lycaenids living within ant nests, but also with a number of species that are obligatorily associated with ants outside their nests in a mutualistic way. Cottrell also discussed possible mechanisms of host-specificity (ant-dependent oviposition, adoption, resource partitioning), but he deferred from the formulation of generalizations since the examples known to him appeared not to be sufficiently worked out.

Recently the hypothesis that the majority of caterpillar-ant interactions are unspecific and facultative received support from a study of DeVries (1991) on myrmecophilous riodinids.

Pierce & Elgar (1985) adopted a totally different view. Based on studies of Australian lycaenids (notably *Jalmenus evagoras*) and a survey of selected literature they concluded that obligatory and specific cases of myrmecophily are rather common among lycaenids in tropical and subtropical regions. In particular, ant-dependent oviposition was assumed to play an important role.

Later on, Pierce (1987) even concluded on the grounds of her literature data that obligate and specific ant-associations are the rule in the southern hemisphere (Australia, India, and southern Africa), while facultative and unspecific associations dominate in the Holarctic region.

However, since the selection of literature data in the papers of Pierce & Elgar (1985) and Pierce (1987) is incomplete and contains a number of doubtful points, the controversy about specificity in lycaenid myrmecophily merits reinvestigation using the broad database given in the Appendix. As a first step, the ants involved in interactions with lycaenids shall be reviewed.

A detailed listing of all cases of lycaenid myrmecophily where the ants involved were determined at least to generic level (field records only) is given in the Appendix (Tab.19). The following Tab.4 gives a condensed overview of how many lycaenid species have been observed associated with each ant genus (limitations of genera following Hölldobler & Wilson 1990). In this latter table, only truly myrmecophilous interactions have been considered. Accordingly, cases where the ants behaved indifferently, or only attended the homopteran food (several Miletinae), were omitted.

When interpreting these tables, one has to be aware of several constraints:

1). In many cases the ants attending lycaenid immatures have not been specified at all.
2). There are undoubtedly misidentifications. Such may be common in taxonomically difficult ant genera where the recognition of sibling species still continues even in well surveyed regions like Europe (e.g. *Myrmica, Lasius*: Seifert 1988 and pers. comm.), whereas the ant genera in most cases should have been determined correctly. However, some doubtful genus records (e.g. *Cataglyphis bicolor* with *Cigaritis myrmecophila*) are omitted from Tab.4.
3). Each ant genus is considered only once for each lycaenid species irrespective of the fact that in a number of cases several ant species of one genus attend the same caterpillar species.
4). The decision whether or not an ant-lycaenid relationship is obligatory, remains uncertain in many cases. Hence, this table gives nothing more than an impression of the diversity of "lycaenophilous" ant genera and their approximate relative importance.

Tab.4: Numbers of Lycaenidae species observed in association with 38 ant genera (field records only). Detailed records see Appendix (Tab.19).

Ant genus	associated lycaenid species	obligate associations
Ponerinae:		
Ectatomma	2	0
Rhytidoponera	1	0
Odontomachus	1	0
Myrmicinae:		
Myrmica	22	6
Pheidole	28	4
Myrmicaria	2	1
Crematogaster	89	41
Monomorium	7	0
Solenopsis	1	0
Meranoplus	1	0
Tetramorium	4	0
Cataulacus	1	0
Dolichoderinae:		
Dolichoderus	6	4
Hypoclinea	1	1
Monacis	1	0
Azteca	1	0
Iridomyrmex	42	20
Tapinoma	21	0
Conomyrma	2	0
Dorymyrmex	2	0
Forelius	1	0
Froggatella	4	1
Technomyrmex	5	0
Engramma	1	0
Formicinae:		
Oecophylla	16	8
Notoncus	3	1
Prolasius	1	0
Acantholepis	6	4
Anoplolepis	10	5?
Plagiolepis	10	0
Brachymyrmex	1	0
Prenolepis	6	0
Paratrechina	3	0
Lasius	27	2
Myrmecocystus	1	0
Formica	33	1
Camponotus	48	15
Polyrhachis	3	0

Several conclusions can be drawn from this table:

1.) Only ant genera that normally exhibit trophobiosis are involved in lycaenid myrmecophily, confirming the findings of Malicky (1969b) and DeVries (1991). The 38 genera documented represent about 12.8 % of the whole generic diversity of the Formicidae (297 genera according to Hölldobler & Wilson 1990), i.e. considerably more than the 20 genera mentioned by DeVries (1991) for Riodinidae and Lycaenidae together.

Strictly predatory ants as most Ponerinae and members of the subfamilies Ecitoninae, Dorylinae, and Leptanillinae never associate with lycaenids, neither do harvester ants (*Pogonomyrmex, Messor* etc.), fungus growers (*Atta*), slave raiders (*Polyergus*), or social parasites.

Four subfamilies have not yet been found associated with lycaenids (i.e. Nothomyrmeciinae, Myrmeciinae, Aneuretinae, and Pseudomyrmecinae), although these are known to collect honeydew or plant nectar.

At least from the Pseudomyrmecinae true trophobiosis is documented (e.g. *Tetraponera*; see Klein 1990), and it seems feasible that associations of lycaenids with members of this subfamily will be detected in the course of future research.

2.) *Crematogaster, Pheidole, Iridomyrmex*, and *Camponotus* are the most species-rich and dominant trophobiotic ant genera on a worldwide scale, and they are the most important partners for lycaenids as well.

The high figures for *Myrmica, Formica*, and *Lasius* are influenced by an "Holarctic bias": these three genera are abundant and often dominant trophobiotic ants in Europe and North America, and since these two regions are best known with regard to lycaenid biology, the high number of records for them is not surprising.

With increasing knowledge of tropical lycaenids, the relative quantitative importance of these three genera should decrease. *Oecophylla*, despite being a very small genus with only two species, is important for lycaenids as well, and this is due to its ecological dominance in many of its habitats. These results are confident with the findings of Malicky (1969b) and DeVries (1991) that dominant trophobiotic ants preponderate in lycaenid-ant interactions.

3.) Obligate lycaenid myrmecophily is only known from 14 ant genera (38.9 % of the 36 genera involved), and only 114 of the 411 lycaenid species (27.8 %) considered in Tab.4 are obligatorily myrmecophilous. These figures are rather difficult to explain. The proportion of obligatorily myrmecophilous lycaenids is almost certainly an overestimate, as will be discussed later.

Ant genera that form large and long-lived societies (e.g. *Crematogaster, Iridomyrmex, Oecophylla*) have the greatest numbers of obligatorily myrmecophilous lycaenids, thus repeating the general pattern known from other myrmecophiles. There are, however, differences among the ant genera that might be important. *Myrmica, Lasius* and *Formica*, for example, have few obligate myrmecophiles among the Lycaenidae. In genera such as *Camponotus, Oecophylla, Crematogaster*, and *Iridomyrmex* about one third to one half of the associated lycaenids are obligate myrmecophiles.

Dolichoderus and *Hypoclinea*, in contrast, have almost exclusively been observed with specific myrmecophiles. Furthermore, records of ant-associations are astonishingly sparse for these two highly trophobiotic genera, suggesting that lycaenids can only maintain associations when specializing towards such hosts using very peculiar mechanisms. Interestingly, *Dolichoderus* and *Hypoclinea* are among the ant genera with the most extreme specializations towards trophobiosis (obligate symbiosis with specific homopterans, true nomadism: Maschwitz & Hänel 1985, Dill 1990).

One should, however, keep in mind that the decision whether or not a given lycaenid is an obligate myrmecophile, is in many cases not yet sufficiently established. Furthermore, ant-associations of lycaenid caterpillars are far more conspicuous, and hence more likely to be reported, if these associations are close and permanent or if the larvae even live inside ant nests.

When lycaenid larvae are only occasionally visited by ants, myrmecophily is more likely to be overlooked. Therefore, the data presented in Tables 4 and 19 are probably biased towards too a high proportion of obligate myrmecophily for both the ant genera and lycaenid species.

4.) In the Polyommatini, at least, several species have a wide range of attendant ants, in some cases 10 or 11 ant species from 3 subfamilies (Myrmicinae, Dolichoderinae, Formicinae). Similar evidence was obtained in laboratory experiments by Malicky (1969b).

Furthermore, in own laboratory trials *Camponotus floridanus* from Florida and a Malaysian *Crematogaster* species attended fourth instar larvae of the Palaearctic *Polyommatus icarus* in the usual way, whereas *Pseudomyrmex mexicanus* from Florida totally ignored caterpillars of the same species without any signs of aggressiveness (Fiedler, unpublished).

These findings indicate that in facultatively myrmecophilous lycaenids the signals the larvae emit are so generalized that nearly any trophobiotic ant species, even from different zoogeographic regions than the caterpillars, may respond adequately to the latter.

Mechanisms of host-specificity

Basically there are two different, but not mutually exclusive possibilities as to how specific lycaenid-ant associations can be founded: either the females select the appropriate host ants for oviposition, or the caterpillars communicate selectively with certain ant species.

The former mechanism (ant-dependent oviposition) was first conclusively demonstrated by Atsatt (1981b) for the Australian *Ogyris amaryllis* and was later on confirmed for *Jalmenus evagoras* by Pierce & Elgar (1985) and Smiley et al. (1988). Pierce & Elgar (1985) provided evidence from the literature that the use of ants as oviposition cues for females of myrmecophilous lycaenids might be widespread.

Their database, however, contains a few inaccuracies:

1). There are some taxonomic errors and misspellings of names (e.g. *Lepidochrysops quassi* assigned to the genus *Catochrysops* [as *phasma*], *Leptotes plinius* assigned to *Tarucus (Castalius)*, i.e. in both cases to unrelated genera).

2.) The claimed specificity of associated ants is not as distinct for *Lachnocnema bibulus* (recorded with *Pheidole, Crematogaster* and *Camponotus*), *Spindasis vulcanus* (recorded with *Crematogaster* and *Pheidole*), *Ogyris amaryllis* (recorded with *Iridomyrmex, Camponotus*, and *Crematogaster*), and *Chilades trochylus* (recorded with *Pheidole, Iridomyrmex*, and *Prenolepis*).

3). Older larvae of *Lycaena rubidus* and, especially, *Chilades trochylus* are steadily associated with ants, contradictory to the statement of Pierce & Elgar.

4). Oviposition substrates and larval hostplants have been confused several times (e.g. for carnivorous Miletinae whose larvae never feed on plants: *Megalopalpus zymna, Lachnocnema bibulus*).

A critical evaluation of the far more complete compilation of literature records given in the Appendix reveals that evidence for ant-dependent oviposition (though often only indirect or anecdotal) is now present for at least 56 species from 27 genera. In extreme cases oviposition may occur on plants that are totally unacceptable for larval nutrition, if only the appropriate host ants are present (e.g. *Anthene emolus* among *Oecophylla* ants on Zingiberaceae: Fiedler, pers. observ.; *Plebejus argus* on bracken, *Pteridium aquilinum*: Mendel & Parsons 1987), but mostly the combination of both hostplants and ants is required.

Detailed investigations of the physiological mechanisms involved in host ant recognition are lacking, but from behavioural observations it can be concluded that visual stimuli are likely to be used in the detection of ant assemblages at a greater range, while the specific recognition is probably mediated by olfactory stimuli at a close range (e.g. Pierce & Elgar 1985, Fiedler & Maschwitz 1989b, c).

Ant nests or trails, or ant-homopteran associations certainly provide sufficient visual cues to be detected by lycaenid females, and the olfactory distinction between various ants based on the diversity of ant pheromones seems feasible, given the excellent ability of most butterfly species to respond specifically to chemical cues of their hostplants.

Observations on species of the genera *Poecilmitis, Aloeides, Erikssonia* and *Anthene* in fact indicate that the females, after having landed near an ant trail, intensively investigate the substrate with the antennae and fore tarsi before oviposition commences (Henning 1983a, 1984, Fiedler & Maschwitz 1989b).

Although ant-dependent oviposition seems not to be a rare curiosity among the Lycaenidae, it has yet been documented almost exclusively in obligately myrmecophilous species (but see the report of Funk 1975 that ovipositing female *Lycaena rubidus* are associated with *Formica altipetens*).

In obligate myrmecophiles ant-dependent oviposition secures the attendance of, or adoption by, appropriate host ants from the beginning of the larval period. Facultatively myrmecophilous lycaenids are almost unknown to show such behaviour, and some

of the records cited in the work of Pierce & Elgar (1985) must be taken with caution (see above). Hence, ant-dependent oviposition is likely to be of more restricted importance than suggested by these authors.

The second way to found specific ant-associations, selective communication of the larvae with its host ants, appears to be less advantageous at the first glance. There is, however, a growing body of evidence that such communication does occur.

As can be seen from the experimental data on larval attractiveness (Malicky 1969b, Ballmer & Pratt in press, this work), different ant species react differentially towards lycaenid caterpillars. This might allow a first step towards specific ant-associations in the course of ecological time: ants stay only with larvae whose secretions are sufficiently attractive.

Lanza & Krauss (1984) and Lanza (1988) demonstrated that different ant genera selectively prefer specific concentration profiles of carbohydrates, amino acids, or peptides in artificial nectars, and the observations of Pierce (1989) strongly indicate that some Australian *Jalmenus* species make use of such specificities. The secretions of these lycaenids differ importantly in their amino acid profiles, and the specific host ants are most strongly attracted by the secretions of "their" appropriate lycaenid trophobionts.

The TOs offer another example of specific reactions of ants towards lycaenid caterpillars, as these organs activate only a part of the large guild of potential trophobiotic ant partners (see above).

However, there is a strong selective disadvantage that all these specificities only gain importance after a caterpillar has been detected by ants. Accordingly, a number of caterpillars might be found by inadequate or even hostile ants. In the case of specific and obligate associations, at least, one would therefore expect that the caterpillars themselves might have evolved mechanisms to locate their host ants. Surprisingly, evidence for this is very incomplete.

Observations on several African Aphnaeini (*Poecilmitis lycegenes, Aloeides dentatis, A. thyra, Erikssonia trimeni, Cigaritis zohra*; Claassens & Dickson 1977, Henning 1983a, 1984, Rojo de la Paz 1990) suggest that these caterpillars follow the pheromone trails of their host ants, but clear experimental evidence is lacking.

Furthermore, the possibility that these caterpillars use their own trail pheromones has not yet been ruled out. The physiological potential for trail-following (and trail-laying) is likely to be present in the Lycaenidae, since both behaviours are known from several Lepidoptera larvae (Lasiocampidae: Weyh & Maschwitz 1978, Peterson 1988; Saturniidae: Capinera 1980; Yponomeutidae: Roessingh et al. 1988), including butterflies (Nymphalidae: Bush 1969; Papilionidae: Weyh & Maschwitz 1982).

Rojo de la Paz (pers. comm.) indeed observed that larvae of *Cigaritis zohra* produce silk trails between the nests of *Crematogaster laestrygon* (wherein they rest during daytime) and their feeding places, and these trails appear to serve as guiding structures. Thus, orientation along ant chemicals may only be used in this species at the very first locating of the ant nest, whereas later caterpillar trails may be used.

In fact, the ant-associations of the above mentioned Aphnaeini species are all first established via ant-dependent oviposition, and trail-following and/or other means of specific chemical communication between caterpillars and ants (e.g. with the TOs) only enhance and stabilize the associations later on. In another very close ant-lycaenid association (*Anthene emolus/Oecophylla smaragdina*) no indication of trail-following by the larvae was obtained (Fiedler & Maschwitz 1989b).

Hence, there seems to exist a general pattern that specific caterpillar-ant association are usually established via ant-dependent oviposition, whereas specific communication between caterpillars and ants, although potentially rather widespread, is less suitable for the foundation of specific and obligate ant-associations within the Lycaenidae. Such communication usually becomes increasingly important after associations have been established.

Two important exceptions from this latter generalization are rather well-known: the genera *Maculinea* and *Lepidochrysops* whose larvae feed on specific hostplants first, but complete their development as predators or parasites in ant nests.

Maculinea larvae leave their hostplants immediately after the moult into the fourth instar and crawl or drop off to the ground. There they wait until they are detected by an ant. Ants of various genera briefly inspect and antennate the larvae, but only *Myrmica* ants intensively palpate them and finally carry them into their nest.

There are significant differences among the *Maculinea* species with regard to the behavioural sequences involved in this adoption process, but usually any *Myrmica* species will adopt the caterpillars of all *Maculinea* species (Thomas et al. 1989, Fiedler 1990b, Elmes et al. 1991a, b; but see Liebig 1989 who reported differential acceptance of *Maculinea alcon* caterpillars by two *Myrmica* species).

There is strong circumstantial evidence that brood pheromone mimics are involved in the adoption of *Maculinea* larvae (Elmes et al. 1991a, b), and the brood odours of *Myrmica* larvae are known to be only genus specific (Brian 1975). However, once arrived in the ant nest, survival of the *Maculinea* caterpillars critically depends on whether or not they have been adopted by an adequate host species of *Myrmica*.

All *Maculinea* species have only a limited number (1—3) of host ant species, and larval mortality is extremely high with inadequate hosts (Thomas et al. 1989, Elmes et al. 1991a, b). The lycaenids, in this case, cannot actively manipulate their chance of being adopted. The findings of Schroth & Maschwitz (1984) that *M. teleius* caterpillars selectively follow *Myrmica* pheromone trails could not be reproduced by Fiedler (1990b). Furthermore, Thomas (1984) and Elmes & Thomas (1987) have observed that *Maculinea* caterpillars always passively await adoption.

Pierce & Elgar (1985) cited old observations of Frohawk indicating that *M. arion* females oviposit in the vicinity of ant nests, but more recent studies of *M. arion, M. teleius*, and *M. nausithous* (Thomas 1984, Elmes & Thomas 1987) could not confirm ant-dependent oviposition.

The only mode how *Maculinea* butterflies can enhance the chance of their offspring being adopted by the right host ants is to stay in the same habitat where they have

developed themselves. In fact, all *Maculinea* species show a tight binding to certain habitats where they usually utilize the most common *Myrmica* species as a host (e.g. *Maculinea arion/Myrmica sabuleti* in dry open grassland with large stands of *Thymus*, *Maculinea nausithous/Myrmica rubra* in moist meadows with *Sanguisorba officinalis*; see Elmes & Thomas 1987, Thomas et al. 1989).

Thus, the establishment of the correct ant-association is a random process in the genus *Maculinea*: the larvae are found by ants only by chance, and it is again a matter of random whether they are adopted by their appropriate hosts.

A system remarkably similar to the *Maculinea/Myrmica* association is that of the African genus *Lepidochrysops* with ants of the genus *Camponotus*. The larvae feed on flowers during the first two instars and are then carried by their host ants into the nests, where they feed on ant brood and regurgitations (Cottrell 1984).

Observations by Cripps (1947) and chemical studies conducted by Henning (1983b) support the hypothesis that mimics of ant-brood pheromones elicit adoption after a typical behavioural sequence. *Lepidochrysops* larvae have never been observed actively entering into ant nests (Claassens 1976).

In most reports of oviposition, no mention is made of ant-dependent hostplant selection (Cottrell 1965, Clark & Dickson 1971, Claassens & Dickson 1980), but Henning (1983b) states that in his laboratory studies the presence of ants was necessary to induce oviposition in *Lepidochrysops ignota*. However, since he obtained very low numbers of eggs, these data are not fully convincing.

In any case, the obligate and specific ant-associations of *Lepidochrysops* larvae are mainly achieved by adoption through the host ants (mediated by pheromone mimics), with ant-dependent oviposition possibly being involved. The larvae again do not actively search their hosts.

Summarizing this chapter, there is strong evidence that ant-dependent oviposition is the main strategy of establishing specific lycaenid-ant associations, while selective communication of the larvae with ants is less important, but does occur. For both mechanisms more detailed studies on a broader range of species are required. In the large number of facultatively myrmecophilous lycaenid species, specific communication plays only a minor, if any role (e.g. ant responses to the TOs).

The obligatory and specific myrmecophiles within the Lycaenidae

Obligate and specific ant-associations are hitherto known or strongly suspected from only a limited number of lycaenid species. The biogeographical distribution of obligate myrmecophily among the Lycaenidae is remarkably uneven (Pierce 1987, and see below), and there is again a strong systematic implication.

In the following, the obligate myrmecophiles are briefly characterized in a systematic arrangement. Obligate ant-associations are unknown from the subfamily Curetinae and from the tribes Poritiini and Lycaenini. Therefore these taxa are omitted here.

Poritiinae

Obligate myrmecophiles are not known from this subfamily with certainty. Observations of Farquharson (1922) and Jackson (1937) indicate that the larvae of some species of the Lipteniti genera *Liptena, Teratoneura, Deloneura, Iridana, Epitola* and *Hewitsonia* only occur on trees infested with *Crematogaster* ants, but direct interactions of these hairy caterpillars with ants have not been reported.

Instead, at least in *Teratoneura isabellae* the ants avoid contacts with the larvae. Possibly some obligate commensalic relationships do exist among the Lipteniti, but this awaits further study.

Miletinae

Obligate myrmecophily is unknown from the Spalgiti and Tarakiti, and is only documented for some Miletiti, Lachnocnemiti and Liphyrini. Five species of *Miletus* have always been found feeding in Homoptera associations tended by *Dolichoderus* ants (old reports of *Polyrhachis* are probably misidentifications), and at least in some cases the females oviposit exclusively when *Dolichoderus* ants are present. However, the caterpillars are largely ignored by the ants, and direct interactions seem to be rare (Eliot 1980, Cottrell 1984, Maschwitz et al. 1985a, 1988).

A similar situation is found in *Allotinus unicolor* where the adults are selectively associated with the ant *Anoplolepis longipes* tending homopterans, while the larvae are again ignored (Maschwitz et al. 1985a, Fiedler & Maschwitz 1989c). The congeneric *A. apries* pupates in ant nests (*Myrmicaria lutea*) and is strongly suspected to live there as a predator from the second instar onwards (Maschwitz et al. 1988).

In the Lachnocnemiti obligate myrmecophily appears to occur in *Thestor*: mature larvae and pupae of several species have exclusively been found in nests of the ant *Anoplolepis custodiens*. Young instars of *Th. basutus* and *Th. protumnus* feed on psyllids or coccids (Clark & Dickson 1971, Migdoll 1988), and the details of the ant-relationships of older *Thestor* larvae remain to be unravelled (predatory on ant brood or on Homoptera in the nests?). Observations on *Lachnocnema bibulus* are controversial. The caterpillars have been found feeding on Homoptera without further attendance of the ants present (Cottrell 1984), but Cripps & Jackson (1940) observed larvae being carried into the nests by *Camponotus* ants; the larvae were even sometimes fed with regurgitations.

In the Liphyrini the caterpillars of *Liphyra* and *Euliphyra* are obligate inhabitants of *Oecophylla* nests where they feed on ant brood (*Liphyra*) or are fed with regurgitations (*Euliphyra*; Hinton 1951, Cottrell 1984, 1987). Oviposition takes place near the host nests. The larvae of the only other Liphyrini genus on which information is available (*Aslauga*) are not truly myrmecophilous, but they are tolerated and ignored when feeding on ant-associated Homoptera.

Lycaeninae

Obligate ant-associations are common among the Aphnaeini. In fact, practically all species of the genera *Aphnaeus, Spindasis, Crudaria, Phasis, Erikssonia, Poecilmitis,*

and *Oxychaeta*, for which sufficient information is available, are obligatorily myrmecophilous. The same is true for most members of *Cigaritis, Axiocerses,* and *Aloeides.* Only in a few species of the latter genera (*Cigaritis allardi, Axiocerses amanga, Aloeides trimeni*) facultative myrmecophily is likely to occur.

In general, the ant hosts belong to the genus *Crematogaster,* but exceptions are documented (*Spindasis vulcanus* and *Axiocerses harpax* also with *Pheidole; Aloeides* and *Erikssonia,* exclusively with *Acantholepis; Axiocerses amanga* and *Poecilmitis pyroeis* with *Camponotus*).

The ant-associations of Aphnaeini are supposedly trophobiotic, the caterpillars providing attractive secretions for their hosts. The larvae of several species are at least sometimes fed with ant regurgitations (surely observed in *Spindasis takanonis* and *Cigaritis acamas,* strongly suspected for *S. nyassae, Axiocerses harpax, A. pseudozeritis*). In some cases, however, available evidence suggests that the larvae may be entirely aphytophagous, possibly feeding on ant brood in nests (*Trimenia, Tylopaedia, Argyrocupha, Oxychaeta*).

Ant-dependent oviposition and specific communication of caterpillars with their host ants (using pheromone mimics from the TOs) are rather well documented in the Aphnaeini. In some species (*Spindasis, Cigaritis, Poecilmitis*) the associations are so close that caterpillars soon die from fungal infections when reared in the absence of their ant hosts, due to the permanent exudation of DNO secretions (Henning 1987, Rojo de la Paz, pers. comm.).

Among the Theclini obligate myrmecophily is less common, but still widespread. Obligatory myrmecophiles are known from four Luciiti genera (*Lucia, Paralucia, Acrodipsas, Hypochrysops*), mostly with the ant genera *Crematogaster* and *Iridomyrmex. Acrodipsas* larvae are even predatory on ant brood throughout their larval period (Samson 1989), while the other genera maintain trophobiotic ant-associations.

In the small subtribes Ogyriti (several *Ogyris* species) and Zesiiti (*Zesius, Jalmenus, Pseudalmenus*) obligate myrmecophily is common as well, but only *Zesius chrysomallus* may occasionally feed on ant brood (Yates 1932). Obligate trophobiotic interactions are known from several Arhopaliti (*Arhopala centaurus, A. pseudocentaurus* with *Oecophylla smaragdina*), and three Malaysian *Arhopala* species feed exclusively on myrmecophytic trees of the genus *Macaranga* (Euphorbiaceae) where they are constantly attended by the specific ant partner *Crematogaster borneensis* (Maschwitz et al. 1984). Further Arhopaliti may turn out to be obligate myrmecophiles, even more so because this species-rich subtribe is yet only fragmentarily known.

Within the subtribe Thecliti only one species (*Shirozua jonasi*) is obligatorily associated with the ant *Lasius spathepus*; the caterpillars feed on aphid honeydew and are supposed to receive ant-regurgitations, thus showing a remarkable life-history parallelism to several Miletinae species.

So, obligate myrmecophily occurs in all but one Theclini subtribes with trophobiotic relationships prevailing. Strictly parasitic interactions are confined to one genus

(*Acrodipsas*), while *Zesius* and *Shirozua* are only partly detrimental to their ant-associates.

Compared to the roughly 530 Theclini species worldwide, the number of obligate myrmecophiles is rather low. A conservative estimate yields distinctly less than 200 obligate myrmecophiles (38 %), assuming that some *Hypochrysops*, all *Philiris*, most Thecliti, and at least half of the Arhopaliti are only facultatively myrmecophilous or even secondarily myrmecoxenous. This assumption is in good accordance with the relative figures among the known life-histories in the Theclini, but may well be an overestimate. The proportion of obligate myrmecophiles is certainly significantly higher in the Aphnaeini ($>$80 %).

In the very large tribe Eumaeini, accounting for one third of the total species diversity of the Lycaenidae, obligate myrmecophiles are almost unknown. Only two closely related *Hypolycaena* species from southern Asia and Australia (*H. erylus, H. phorbas*) are apparently obligatorily associated with *Oecophylla smaragdina* in a trophobiotic way.

From the more than 1000 Eumaeiti species not a single obligate ant-association is hitherto sufficiently documented, nor is any species with ant-parasitic life-habits known. Notwithstanding the scanty knowledge of the larval biology of the Neotropical Eumaeiti, in particular, it is clear that the proportion of obligate myrmecophiles is very low ($<$ 10 %) within the Eumaeini.

In the Polyommatini, obligate myrmecophily is again restricted to a few taxonomic groups. In the Lycaenesthiti, several *Anthene* and *Triclema* species maintain obligate trophobiotic ant-associations, and one (*A. levis*) is even fed by regurgitations of *Crematogaster* ants.

Similarly, the only Niphanditi species whose life-history is known (*Niphanda fusca*) is fed by its specific host ant, *Camponotus japonicus*.

The large subtribe Polyommatiti has two genera with well-documented obligate myrmecophily, the parasitic *Maculinea* and *Lepidochrysops* (see above). Two species of the *Polyommatus* section (*Plebejus argus* and *P. idas*) have recently been shown to maintain quite specific and possibly obligatory trophobiotic ant-associations (e.g. Jutzeler 1989d, e, Ravenscroft 1990), and in some Oriental *Tarucus* species (*T. waterstradti, T. ananda, T. nara*) there is some evidence for obligate myrmecophily as well (Hinton 1951, Maschwitz et al. 1985b).

Assuming that less than one third of the Lycaenesthiti, all Niphanditi, the genera *Maculinea* and *Lepidochrysops*, and a further dozen of Polyommatiti species in other groups are obligatorily myrmecophilous, the proportion of obligate myrmecophiles is well below 200 species (17 %).

Summarizing the current evidence, there is a distinctive systematic disparity with regard to the distribution of obligate myrmecophily in the higher lycaenid taxa. While obligate associations preponderate in the Aphnaeini, and are reasonably common in some Theclini and Miletinae groups, obligate myrmecophily is restricted to very particular taxa in the Polyommatini and is almost entirely unknown from the Eumaeini.

Evidence for obligate ant-associations, often very indirect, is available for only 200 species out of 1000 (20 %) with life-history information available (see Appendix, Tab.17 and 19). Extrapolating on the whole family, most likely less than 800 lyceanid species (< 20 %) are obligatorily associated with specific ants.

It must be emphasized that the estimates presented here are all conservative with respect to the hypotheses of Pierce (1987), i.e. they rather assume too a high proportion of obligate myrmecophily. Obligate ant-associations may well be considerably less numerous in the Theclini and Polyommatini. Nevertheless, single obligatorily myrmecophilous lycaenid taxa are rather species-rich (Aphnaeini, *Lepidochrysops*) and it is plausible to assume that in these taxa the specialization on certain host ants has strongly influenced the evolution, resulting in either a great hostplant range (Pierce & Elgar 1985) or a more rapid speciation (Pierce 1984).

However, as will be discussed in the next chapters, these mechanisms are unlikely to apply for the facultatively myrmecophilous or myrmecoxenous lycaenids, which account for the majority of species (> 75 %).

LYCAENID HOSTPLANT RELATIONSHIPS AND MYRMECOPHILY

Hostplants as selective agents in the Lycaenidae

Myrmecophily of lycaenid caterpillars is mainly mediated by the energetically costly secretions of three types of exocrine epidermal glands (PCOs, DNO, TOs): carbohydrates and amino acids in the DNO secretions (e.g. *Jalmenus, Glaucopsyche, Polyommatus*); possibly amino acids in the PCO secretions (*Glaucopsyche lygdamus* pupae), or ant-brood pheromone mimics in other taxa (e.g. *Lepidochrysops, Maculinea*); and supposedly ant-alarm pheromone mimics from the TOs.

Development and maintenance of the ant-organs (including associated muscles, neurons, cuticular structures etc.) impose additional costs to ant-associated lycaenid caterpillars. The few cost-benefit studies available indeed demonstrated that myrmecophily and its related secretions may result in pupation at a lower final weight associated with reduced fecundity (*Jalmenus evagoras*: Pierce et al. 1987, Elgar & Pierce 1988), or in a prolonged larval period (*Arawacus lincoides*: Robbins in press; see also Henning 1984b).

All energy necessary for both larval development and myrmecophily must be derived from the larval food, viz. usually hostplants. Given these constraints, Pierce (1985) and Pierce & Elgar (1985) have thus argued that the hostplant selection of lycaenids should be strongly influenced by their myrmecophilous life-habits. The idea that hostplant selection could be modified in myrmecophilous species has been presented earlier (e.g. Ehrlich & Raven 1964), and Atsatt (1981b) has shown that *Ogyris amaryllis* females even chose nutritionally inferior hostplants to secure the attendance of specific ants.

Two major hypotheses have been proposed with regard to the possible trade-offs between hostplant selection and lycaenid myrmecophily: the "preference" and the "amplified host range" hypothesis.

The "preference hypothesis"

According to Pierce (1985) myrmecophilous species should tend to utilize energy-rich (and, in particular, protein-rich) hostplants. She proposed that nitrogen-fixing plants from the order Fabales (legumes), parasitic plants from the order Santalales (e.g. mistletoes), or young growth and reproductive plant tissues should be the favourite larval food for ant-associated lycaenids. A widespread predilection of legumes or young growth as larval food in the Lycaenidae has been noted earlier (e.g. Ehrlich & Raven 1964, Cottrell 1984).

Pierce's proposal was substantiated with literature data on the biology of c. 300 species, and recent experiments have confirmed that the quality of larval nutrition may be decisive in maintaining ant-associations. Larvae of *Polyommatus icarus* reared on the legume tree *Robinia pseudoacacia* (a non-host poorly fitting to the nutritive requirements) were far less attractive to ants than those fed herbaceous Fabaceae hostplants (Fiedler 1990c). *Jalmenus evagoras* caterpillars reared on hostplants fertiliz-

ed with additional nitrogen sources became more attractive to ants than those on un-treated trees, and the females even preferred such plants for oviposition (Baylis & Pierce 1991).

The "amplified host range hypothesis"

Pierce & Elgar (1985) suggested that myrmecophilous lycaenids should tend to utilize a wider range of hostplants than myrmecoxenous ones, at least in those species where the specific ant-associations are of paramount importance for larval survival. In such species oviposition should largely depend on the presence of appropriate ant partners, and a strong selection for an amplified host range was predicted, with a possible pathway towards speciation (Pierce 1984). Again, literature data were compiled to support this amplified host range hypothesis.

In both studies, however, systematic aspects were neglected, although hostplant rela-tionships among the Lepidoptera are often astonishingly conservative in given systematic groups. While switches in larval hostplants do occur regularly, they in many cases involve either phylogenetically related or chemically similar plant species, sug-gesting that correlations between hostplant use and phylogeny are common.

Accordingly, attempts have been made to incorporate hostplant relationships in systematic investigations on Lepidoptera (e.g. Downey 1962b), and the concept of coevolution (Ehrlich & Raven 1964) was originally based on the hostplant relationships of butterflies. The theory of coevolution has been the subject of considerable debate ever since, and the unique role of semiochemicals in the formation of plant-herbivore associations has been questioned repeatedly (e.g. Smiley 1985).

Nevertheless, empirical data on hostplant relationships within the Lepidoptera have very often corroborated the existence of phylogenetic patterns. Many subgroups of the largest butterfly family Nymphalidae, for example, are centred on particular taxonomic plant groups (Ackery 1988), or they utilize hostplants that have special semiochemicals in common (Edgar 1984).

The Papilionidae and Pieridae subfamilies and tribes likewise possess characteristic hostplant relationships (e.g. Zerynthiini and Troidini on Aristolochiaceae, Papilionini on Rutaceae and Apiaceae, Dismorphiinae and Coliadinae on Fabales, Pierinae on Capparales), and in these two families secondary plant compounds (glucosinolates, alkaloids etc.) are known to play a leading role in taxon-specific host relations.

Hostplant relationships and food preferences of the Lycaenidae have rarely been used in classificatory attempts, and few authors have tried to cover the whole spectrum of that large family. Ehrlich & Raven (1964) recognized that lycaenids utilize a very broad spectrum of hostplants, approximately equally diverse as that of the more species-rich Nymphalidae. They described only few, rough systematic hostplant patterns (e.g. Ly-caenini on Polygonaceae, Thecliti on Fagaceae, Polyommatini on Fabaceae), but this is not amazing given the scanty knowledge of lycaenid life-histories and the lack of a more realistic classification at that time.

The "bewildering array" of lycaenid hostplants largely prevented Ehrlich & Raven and later authors from more detailed analyses, and subsequent studies (Vane-Wright 1978,

Cottrell 1984, Pierce 1985, Ackery 1988) basically adopted Ehrlich's and Raven's view.

With the growing knowledge of lycaenid hostplants, however, several of Ehrlich's and Raven's statements have proven wrong (e.g. lycaenids are now known to utilize ferns, Begoniaceae, Bignoniaceae, Celastraceae, Cucurbitaceae, Myrtaceae, or Rubiaceae as hosts), and today a distinctly broader database concerning lycaenid hostplants is available.

Thus, it seems necessary to reinvestigate in more detail whether or not systematic patterns of hostplant use do occur in the Lycaenidae or in some of their subgroups. If so, these instead of selective pressures arising from myrmecophily might account for a considerable proportion of the extant pattern of hostplant use in that family. Detailed discussions on the hostplants and ant-associations of the Riodinidae were given by Harvey (1987) and DeVries (1990b).

In this chapter I will address the following questions: Do the subfamilies, tribes, subtribes etc. of the Lycaenidae exhibit taxon-specific trends in their hostplant relationships? Do myrmecophilous species really tend to prefer plants of the Fabales or Santalales as suggested by Pierce (1985)? And, do myrmecophilous species really show the amplified hostplant range as predicted by Pierce & Elgar (1985)?

Database and analytical procedure

From more than 200 literature sources I extracted the information concerning larval hostplants (only considered here at family level), ant-associations, and the presence of myrmecophilous organs for more than 1000 lycaenid species. Endophytic feeding habits or preferences for young growth, flowers, or ripening seeds were also noted.

This literature survey was intended to cover the whole systematic spectrum of the Lycaenidae as complete as possible. Since the extensive literature on butterfly hostplants perpetuates a huge number of erroneous records, special attention was paid to include only reliable data into the analysis, although certainly some erroneous records have found their way here again.

The data obtained are of very different quality, ranging from mere oviposition records to detailed ecological studies. To reduce the unevitable bias arising from this, I have considered oviposition records or observations from laboratory rearings only, if closely related species are definitely known to utilize similar plants in nature. Foodplant records from laboratory rearings (a minority) are included because they help demonstrating the physiological potential of the respective species.

Furthermore, the knowledge of lycaenid hostplants is still much less complete than in families like Papilionidae or Nymphalidae, and the distribution of hostplant records is rather uneven among the higher taxa of the Lycaenidae. In total, life-history information was obtained for less than 25 % of the described species, but some species-rich higher taxa (Poritiinae, Arhopaliti, *Jamides* and *Lycaenopsis* section of the Polyommatiti) are distinctly under-represented.

Nevertheless, the database presented in the Appendix is assumed to be sufficiently complete to support the detection of realistic patterns. An increasing knowledge of lycaenid larval biology will certainly modify, but in all probability not reverse these patterns.

To allow quantitative comparisons among the hostplant relationships of the higher Lycaenidae taxa, the hostplant range of the larvae was scored using the number of hostplant families (family index FI; delimitations of plant families following Ehrendorfer 1983) as well as a categorization into the following 5 ranks (range index RI):

1: monophagous (one hostplant species only); 2: stenoligophagous (one hostplant genus); 3: oligophagous (one hostplant familiy); 4: moderately polyphagous (hostplants in two families); 5: polyphagous (hostplants in three or more families).

For all subfamilies, tribes and subtribes the arithmetic means and standard deviations of FI and RI are calculated. These indices facilitate comparisons with the respective figures of Pierce (1985).

In view of the fragmentary knowledge of many lycaenids such a scoring and analysis is necessarily a rough approximation. An analysis using the number and taxonomic relatedness of hostplant species would certainly be more appropriate, but is yet impossible on a worldwide scale.

A detailed survey of the evolution and physiology of hostplant relationships of the Lycaenidae is beyond the scope of this study and requires more complete data. Even for the rather well known Holarctic fauna additions to the hostplant lists are permanently recorded, but new family records are relatively rare.

Thus, the family index FI gives a more reliable, albeit rough estimate of the hostplant spectrum of a butterfly species. A disadvantage of FI is that a few species with exceptional polyphagy (e.g. *Hypochrysops ignitus, Callophrys rubi, Strymon melinus, Celastrina argiolus*) may bias the average FI of a particular taxon. As a consequence, the variance of FI is usually high. This is partly compensated by using the range index RI where the coefficient of variation (the ratio of standard deviation and arithmetic mean) never exceeds 0.54 (up to 1.47 with FI).

On the grounds of this descriptive treatment of lycaenid hostplant relationships I then examine possible trade-offs with myrmecophily. Unfortunately, the presence or absence of preferences for young growth or inflorescences is only sporadically indicated in the literature. Accordingly, this potentially important characteristic had to be excluded from the quantitative analyses. The distribution of host ranges (RI), and the predilection of legumes or mistletoes, are related to the information available on myrmecophily in contingency tables.

Since the records of ant-associations are incomplete in many (especially tropical) taxa, I have tentatively treated such species as myrmecophiles as well, if appropriate information on closely related species is present. These myrmecophily estimates are always conservative, and the strong correlations between phylogeny and ant-associations validate this procedure (see also Fiedler 1991).

A more detailed analysis including the degree of myrmecophily (definitions see Fiedler 1991 and Tab.17 in the Appendix) was omitted in view of the sketchy database.

Quantitative evaluations were normally carried out computing Chi² statistics (with Yates' correction). For small "sample sizes" (= species numbers) Fisher's "exact probability" was calculated. Similar analyses were conducted by Pierce (1985) and Pierce & Elgar (1985).

It must, however, be kept in mind that the life-history data only partially fulfill the requirements of a statistical analysis. The Holarctic *Polyommatus* group, for example, is much better known than the equally diverse Oriental subtribe Arhopaliti, exemplifying the distinct Holarctic bias in the recording of lycaenid life-histories. Despite this partial non-randomness of the data, a statistical approach may be helpful in disentangling the complex patterns observed.

The hostplant relationships of the higher lycaenid taxa

Aberrant feeders: Poritiinae and Miletinae

These two subfamilies exhibit striking larval feeding habits largely deviating from the usual herbivory of most lepidopterous caterpillars. The Poritiinae consist of two tribes, one of which, the Oriental Poritiinae, are herbivores of trees (information found only for 1 of c. 50 species).

In contrast, the larvae of the African Liptenini (information found for 58 of the c. 520 spp.) feed on lichen, fungi and similar substrates (throughout this chapter I omit the citations of references to facilitate use; all references used are given in Tab.17 and 19 in the Appendix).

With the possible exception of some Lipteniti whose larvae have always been observed on trees heavily infested with *Crematogaster* ants, Poritiinae caterpillars are strictly myrmecoxenous. Since these presumed myrmecophiles feed on the same substrates as their myrmecoxenous counterparts, no evidence for effects of myrmecophily on larval nutrition can be found among the Liptenini. As the taxonomic host ranges of most of the lichen feeders are unknown, a discussion of the host range hypothesis must be deferred.

The specialization on lichen or fungi, however, may be an important prerequisite for one evolutionary route leading to myrmecophily: caterpillars able to feed on such substrates are physiologically adapted to metabolize chitin (which is an important compound of fungi; cf. Rawling 1984) and may start to utilize fungi or even remains of ants in ant nests. The lichen-feeding arctiid moth *Crambidia casta* could represent a parallel case for this evolutionary route towards myrmecophily (Ayre 1958).

Miletinae larvae (information found on 37 of c. 140 spp.) are entirely aphytophagous, feeding on Homoptera, ant brood, honeydew, or ant regurgitations. Only part of the Miletinae caterpillars are undoubtedly myrmecophilous, but these utilize basically similar and equally protein-rich food-substrates as their myrmecoxenous relatives.

Consequently, no trade-offs between larval food and degree of myrmecophily can be observed. Some Miletinae species (e.g. *Allotinus unicolor, Miletus* spp.) are specifically

associated with certain ants and are presumed to feed on a rather broad variety of Homoptera (Maschwitz et al. 1988, Fiedler & Maschwitz 1989c). However, since most obligatorily myrmecophilous Miletinae are predators or parasites of their specific host ants only, this evidence supporting the host range hypothesis is very limited. The carnivorous feeding habits of Miletinae immatures provide a set of preadaptations for another independent pathway leading to myrmecophily (Cottrell 1984, this study).

The remaining lycaenid subfamilies are primarily herbivorous, and a meaningful discussion of the hypotheses of Pierce (1985) and Pierce & Elgar (1985) has to be restricted to them.

Curetinae

This small group feeds almost exclusively on legumes (information found for 6 of the 18 spp.; RI = 3.17 ± 0.41 , FI = 1.17 ± 0.41) with strong preference for young growth (DeVries 1984, Maschwitz & Fiedler, unpublished). These are exactly the conditions where myrmecophily should be expected according to Pierce (1985). However, *Curetis* larvae are not truly myrmecophilous, as has been explained in detail above.

Lycaeninae

This large subfamily contains more than 3,640 species, i.e. more than 80 % of the whole species diversity of the family Lycaenidae. Because of this and the large heterogeneity of several groups with regard to their feeding preferences and myrmecophilous relationships, the tribes and subtribes will be treated separately.

A p h n a e i n i — Larvae of this mainly African tribe (information present for 77 of about 250 spp.) utilize a broad range of at least 32 hostplant families. Thirty-eight species feed on legumes (at least in captivity), other well-represented plant families are Zygophyllaceae (16 species) and Asteraceae (13 species; both mainly in the genus *Poecilmitis*). Plants of the order Santalales are mentioned as larval food for only five species.

Several members of the Aphnaeini are known or at least strongly suspected to be aphytophagous; five species of the genera *Spindasis, Cigaritis* and *Axiocerses* are fed by *Crematogaster* ants with regurgitations, *Oxychaeta dicksoni* seemingly feeds on *Crematogaster* brood, and the genera *Tylopaedia, Trimenia* and *Argyrocupha* are suspected to be entirely aphytophagous.

Aphnaeini larvae exhibit an extraordinarily high degree of myrmecophily. No single species is known to be myrmecoxenous, but as many as 80 % of the species where information is present are strongly or even obligatorily associated with ants.

Although the Aphnaeini are among the most strongly myrmecophilous lycaenids, and nutritive liquids are secreted by the larvae of some species in high amounts, a correlation between larval hostplants and ant-associations is not apparent. For example, legumes are only weakly represented in the hostplant list of the obligately myrmecophilous genus *Poecilmitis* and are not used by *Phasis* at all.

About half of the myrmecophilous Aphnaeini species are not associated with legumes. However, the taxonomically widespread use of Fabales as hosts indicates that these may be the primary hostplant group of the tribe. The statistical evaluation shows (Tab.5) that obligatorily and facultatively myrmecophilous Aphnaeini species do not differ in their use of legumes as hosts. A preference for young growth or flowers has been reported for only 10 species suggesting that this trend is not well developed in the Aphnaeini. So, the predilection hypothesis does not apply to this tribe, nor does the host range hypothesis.

Most Aphnaeini species are confined to one foodplant family, while only 20 (including 7 laboratory records) have been reported to utilize at least two plant families (RI = 2.72 ± 1.20; FI = 1.53 ± 1.09; n = 71 herbivorous species). The host ranges of obligatory and facultative myrmecophiles among the Aphnaeini cannot be distinguished statistically (Tab.5).

Rather, there appears to exist a systematic pattern: polyphagous species within the Aphnaeini mainly occur in the genera *Spindasis* and *Poecilmitis*, whereas species of *Cigaritis, Axiocerses, Phasis* and *Aloeides* tend to be oligophagous, suggesting that the former two have a better developed potential for polyphagy, whereas the latter four are basically food specialists. The high degree of myrmecophily, however, does not differ between these taxa.

Tab.5: Host range (range index RI 1—3 versus 4/5), association with legumes, and myrmecophily in the lycaenid tribe Aphnaeini (obl: obligate myrmecophiles, fac: facultative myrmecophiles). Given are absolute species numbers (database see Appendix). Test statistics for 2x2 contingency tables: Fisher's exact probability (P).

RI	1—3	4/5	P
obl	48	16	> 0.8
fac	5	3	

hostplants	Fabales	other plants	P
obl	32	31	> 0.8
fac	5	3	

L y c a e n i n i — This small tribe of nearly worldwide distribution has very homogeneous hostplant relationships. The larvae feed primarily on Polygonaceae (information found for 38 of c. 95 spp.) with exceptions known from only six Nearctic species (on Rosaceae, Ericaceae, Rhamnaceae, Grossulariaceae). Doubtful records include Fabaceae (*Lycaena thersamon*) and Chenopodiaceae (*L. phoebus*, oviposition record only). At least for one group of closely related species (*Lycaena helloides/dorcas*), the hostplant shift from Polygonaceae to Rosaceae is correlated with similar allelochemicals in the plant species involved (Ferris 1979).

The hostplant range of all species is narrow, normally covering only one plant genus (RI = 2.08 ± 0.59, FI = 1.03 ± 0.16, n = 38). European Lycaeninae larvae are usually

myrmecoxenous and ant-associations have only exceptionally been observed (*Lycaena dispar*: Cottrell 1984). Other *Lycaena* caterpillars (*L. virgaureae, ottomanus, alciphron, hippothoe, phlaeas, tityrus*) sometimes induce ant-associations in the laboratory (Malicky 1969, this study), but this has not been confirmed in the field.

Only four Nearctic species are regularly attended by ants (*L. heteronea, L. rubidus, L. xanthoides, L. editha*: Ballmer & Pratt 1988). All these species feed exclusively on foliage of Polygonaceae, and there is no indication of any trade-offs between hostplant use and the low level of myrmecophily in a couple of species among the Lycaenini. Neither the predilection nor the host range hypothesis receives support from the hostplant relationships of this tribe.

Theclini

Luciiti

The Theclini comprise about 530 species in 5 subtribes with biological information available for 120 species. The Australian Luciiti (c. 150 spp., information found for 43) utilize a remarkably large spectrum of at least 36 hostplant families, including ferns (*Hypochrysops theon*), monocots (Dioscoreaceae: *Pseudodipsas, Hypochrysops*), and Lauraceae (*Philiris* spp.). Legumes and parasitic plants of the order Santalales are only weakly represented as hosts (four species each).

A general hostplant pattern of the Luciiti is not yet apparent, but several genera show specific feeding habits: *Paralucia* on Pittosporaceae, *Philiris* on Lauraceae, Urticales and Euphorbiaceae. *Acrodipsas* larvae are predators of *Crematogaster* and *Iridomyrmex* brood. *Pseudodipsas* and *Hypochrysops* are polyphagous genera, *H. ignitus* alone being recorded from 17 plant families.

The caterpillars of all genera but *Philiris* are usually myrmecophilous, several species in the genera *Lucia, Paralucia, Pseudodipsas, Acrodipsas* and *Hypochrysops* even obligatorily so. However, as already mentioned by Valentine & Johnson (1989), there is no indication of a preference for protein-rich hostplant families in the myrmecophilous Luciiti, and this view is corroborated by the statistical evaluation of the life-history information (Tab.6).

Actually all Luciiti species feeding on legumes or mistletoes are myrmecophilous, while no myrmecoxenous species are known to feed on these plants. But this result is only marginally statistically significant for legumes plus mistletoes (Fisher's P = 0.058), and not at all significant for legumes alone. A predilection of young growth is only recorded from three genera (*Paralucia, Pseudodipsas, Hypochrysops*).

The host range hypothesis receives more support in the Luciiti. On average, Luciiti larvae are moderately polyphagous (RI = 2.41 ± 1.31; FI = 2.16 ± 3.18; n = 38 phytophagous spp.). Host ranges of obligatory and facultative myrmecophiles are similar, but polyphagous species exclusively occur among the myrmecophiles, whereas the myrmecoxenous members of *Philiris* are apparently all confined to one hostplant familiy or even genus (Tab.6; see also Valentine & Johnson 1988, 1989).

Nevertheless, this host range difference is again just marginally significant, and polyphagy is recorded from only seven species of *Pseudodipsas* and *Hypochrysops*, while 21 myrmecophilous Luciiti species have thus far been reported from one single hostplant family. So, it is well possible that the amplified hostplant ranges of *Pseudodipsas* and *Hypochrysops* indicate a phyletic predisposition for, rather than a consequence of, ant-dependent foodplant choice.

Tab.6: Host range (range index RI 1—3 versus 4/5), association with legumes, and myrmecophily in the lycaenid subtribe Luciiti (obl: obligate myrmecophiles, fac: facultative myrmecophiles, phil: all myrmecophiles, xen: myrmecoxenous species). Given are absolute species numbers (database see Appendix). Test statistics for 2x2 contingency tables: Fisher's exact probability (P).

RI	1—3	4/5	P
obl	11	4	> 0.8
fac	9	3	
phil	20	7	0.058
xen	12	0	

hostplants	Fabales	other plants	P
obl	3	12	0.61
fac	1	11	
phil	4	23	0.21
xen	0	12	

Ogyriti

This small Australian tribe contains only 15 species, the life-histories of 12 being known. All utilize Loranthaceae or the closely related Santalaceae as hostplants, thus showing a remarkably homogeneous hostplant range (RI = 2.50 ± 0.52; FI = 1.00 ± 0.00; n = 12). This strongly suggests a taxon-characteristic and evolutionarily stable adaptation towards similar allelochemicals of the Santalales.

Probably all Ogyriti larvae are ant-associated and possess a full complement of ant-organs, with some species (e.g. *Ogyris genoveva, O. otanes, O. amaryllis*) probably being obligatorily myrmecophilous. At least one species, *O. amaryllis*, uses ants as oviposition cues (Atsatt 1981b). The confinement of Ogyriti to Santalales as hostplants agrees well with the preference hypothesis of Pierce (1985), but gives no support to the amplified host range hypothesis.

Zesiiti

This subtribe comprises 11 species in southern Asia and Australia with life-history information available for all of them. Zesiiti larvae feed on legumes, but four species utilize additional families (*Zesius*: Combretaceae, Dioscoreaceae; *Jalmenus*: Sapindaceae, Myrtaceae). The hostplant range (RI = 2.82 ± 1.47; FI = 1.73 ± 1.01; n = 11) is moderate.

All Zesiiti are myrmecophilous, at least half of them even obligatorily so. The ant-associated Zesiiti show the preference for nitrogen-fixing plants and young plant tissue postulated by Pierce (1985), and the experimental work of Baylis & Pierce (1991) clearly demonstrates the importance of the nutritive quality of larval food for maintaining ant-associations.

However, the Zesiiti hostplant pattern does not consistently support the amplified host range hypothesis. While some of the obligatorily myrmecophilous species utilize several plant families (*Zesius chrysomallus, Jalmenus ictinus, J. pseudictinus*), others are clearly confined to a single plant genus (*J. evagoras, Pseudalmenus chlorinda* on *Acacia*). In all, the Zesiiti hostplant pattern is indicative of a primary association with young growth of legumes and some secondary amplifications towards Sapindaceae, Combretaceae or Myrtaceae.

Interestingly the same plant families are utilized by several other lycaenids feeding primarily on Fabales (*Hypolycaena, Deudorix, Anthene*) and also by the nymphalid tribe Charaxini (Ackery 1988), suggesting that the chemical barriers opposing these particular hostplant shifts are low.

Arhopaliti

This large tribe contains about 240 species with peak diversity in South East Asia. Information on larval biology (20 spp. only) is very scanty. Hostplant families include Fagaceae and Euphorbiaceae (both for six species), Myrtaceae, Lythraceae and Combretaceae (each for four species), totalling 13 families. Legumes and mistletoes are mentioned for only one species each.

Facing this fragmentary knowledge, the only tentative statement yet possible is that Arhopaliti larvae feed upon a wide range (RI = 3.06 ± 1.66; FI = 2.00 ± 1.66; n = 16) of broad-leaved trees, apparently preferring young growth, but neither predilecting Fabales nor Santalales.

Myrmecophily seems to be the rule in the Arhopaliti, and some members are obligatorily associated with a single ant species (e.g. *Arhopala centaurus, A. pseudocentaurus* with *Oecophylla smaragdina*). These two *Arhopala* species are highly polyphagous and may provide examples for the amplified hostplant range in response to obligate and specific ant-associations. Three other *Arhopala* species, in contrast, are monophagous on myrmecophytic *Macaranga* trees (Euphorbiaceae) where they live in close association with the appropriate symbiotic ant of these trees, *Crematogaster borneensis*. Hence, specific ant-associations in the genus *Arhopala* are not necessarily correlated with a wide hostplant range.

The current poor knowledge of Arhopaliti biology precludes any conclusive discussion of this subject, while the preference hypothesis is not at all supported by the data available.

Thecliti

The larval biology of this predominantly Asiatic subtribe is considerably better known (information found for 34 of c. 120 species). As was already pointed out by Shirôzu

(1962), the primary Thecliti hostplant family are the Fagaceae, reported as hosts for 22 species (including laboratory records).

Additional related plant families of the Hamamelididae (Hamamelidaceae, Betulaceae, Corylaceae, Myricaceae, Juglandaceae, Ulmaceae) are utilized by some species. One group of related genera feeds on Oleaceae. Rather exceptional are the associations with Rosaceae (*Thecla, Chrysozephyrus smaragdinus*) or Ericaceae (*Chrysozephyrus birupa*). *Shirozua jonasi* feeds on aphids and regurgitations of the ant *Lasius spathepus*, and the taxonomically isolated *Amblopala avidiena* is the only Thecliti species reported from legumes.

Hence, although 12 plant families are involved, the hostplant associations of the Thecliti show a distinct pattern: a predilection of Hamamelididae trees (mainly Fagaceae) which typically contain high amounts of tannins and often possess ethereal oils. Interestingly the unrelated Eumaeiti genus *Satyrium* s. l. shows a parallel hostplant pattern with 11 species on Hamamelididae, 10 on Rosaceae, and two on Ericaceae and Oleacae, suggesting that chemical similarities have independently governed the evolution of hostplant use in these two taxa of temperate woodlands.

The hostplant range of most Thecliti species is rather narrow (RI $= 2.56 \pm 1.05$; FI $= 1.32 \pm 0.84$; n $= 34$), and at least some species preferentially or exclusively feed on young growth or reproductive tissues of their hosts. Several of the records cited by Shirôzu (e.g. for *Thecla betulae* and *Quercusia quercus*) are only rare occasional hostplants or result from laboratory findings, because these two Palaearctic species are usually known from Europe to utilize only one plant family in nature (Rosaceae and Fagaceae, respectively).

Most Thecliti larvae lack the typical ant-organs, and records of ant-associations are rare among this subtribe except for some old reports of ant-associations of *Thecla betulae* (Malicky 1969; possibly derived from artificial trials: Emmet & Heath 1990). However, ants attend pupae of *Thecla betulae* and *Quercusia quercus* (Emmet & Heath 1990), and *Shirozua jonasi* is obligatorily myrmecophilous. Anyway, since most Thecliti exhibit only a low degree of myrmecophily, a discussion of the preference or host range hypothesis within this subtribe would be misplaced. *Amblopala avidiena* appears to be the only known Thecliti species possessing a DNO and TOs. This morphological trait and the hostplant relationship with legumes challenge its current systematic position.

Thecliti and Arhopaliti are presumed to be sister-groups (Eliot 1973). Interestingly, Fagaceae are well represented among their hostplants and both show no preference for legumes. This common hostplant pattern supports the idea that Thecliti may be derived from Arhopaliti-like ancestors. The subsequent reduction of myrmecophily among the Thecliti might then be attributed to the rather poor nutritive quality of Fagaceae trees in concert with the relative paucity of ants foraging in the canopy of temperate zone woodlands.

The hostplant pattern of Theclini as a whole is rather obscure, and this again emphasizes the heterogeneity of this taxon of questionable monophyly. Fifty hostplant families are utilized by 111 species for which adequate information is available. Twenty-

eight species feed on Fagaceae, 17 on legumes, 15 on Loranthaceae, 11 on Euphorbiaceae, 10 on Myrtaceae, 8 on Sapindaceae and Combretaceae, 7 on Oleaceae, 6 on Lauraceae and Verbenaceae, and 5 on Rosaceae. Twenty hostplant families are hitherto recorded for only one single Theclini species. This is indicative of an overall high diversity of larval hosts (mainly broad-leaved trees and shrubs or epiphytes, rarely non-woody plants), in particular among the most diverse subtribes Luciiti and Arhopaliti.

The majority of Theclini larvae are oligophagous (RI = 2.60 ± 1.23, FI = 1.68 ± 2.06, n = 111). Only 22 species are recorded from two or more hostplant families (Tab.7), but polyphagy is significantly more common among the myrmecophiles. However, there is no difference in the host range between obligate and facultative myrmecophiles, as would be expected if ant-dependent hostplant selection were the primary selective force towards polyphagy.

A predilection of Fabales or Santalales only exists in small subgroups (Ogyriti, Zesiiti). All species feeding on these plants are myrmecophilous, while myrmecoxenous Theclini consistently use other plant families as larval hosts. This results in a statistically significant difference between the hostplant associations of myrmecophilous and myrmecoxenous Theclini (Tab.7), but with respect to the scant information and the systematic trends outlined above generalizations should be taken with caution.

Although the preference hypothesis of Pierce (1985) receives some support when viewing on the whole tribe Theclini, more than half of its myrmecophilous members are not known to feed on Fabales or Santalales. Remarkably, there is no Theclini subtribe to which both the preference and host range hypothesis consistently apply. Myrmecophilous Ogyriti and Zesiiti predilect Fabales and Santalales, but are mostly oligophagous. In contrast, the myrmecophilous Luciiti and Arhopaliti, albeit rather polyphagous, do not utilize the postulated plant taxa to a greater extent.

Eumaeini

The Eumaeini are by far the largest lycaenid tribe with c. 1.580 described species. The monophyly of this grouping (sensu Scott & Wright 1990) is not sufficiently confirmed, and its subdivision is far from being satisfactory. In addition, the predominantly Neotropical Eumaeeiti (the largest subtribe with over 1.000 species) are poorly known with regard to their taxonomy and larval biology. Thus, the following discussion of Eumaeini hostplant patterns and myrmecophily is necessarily tentative.

Catapaecilmatiti

This small Oriental tribe comprises only 11 species in two genera. Information is only available for *Catapaecilma* whose highly myrmecophilous larvae feed on young shoots of Combretaceae, thus neither confirming the preference nor the host-range hypothesis.

Amblypodiiti

A small Palaeotropical group (c. 13 species, information available on 8), feeding on young growth of Olacaceae (*Amblypodia*) or Moraceae (*Iraota, Myrina*). The larvae possess a DNO and TOs and are usually myrmecophilous. The ant-associations

Tab.7: Host range (range index RI 1—3 versus 4/5), association with legumes, and myrmecophily in the lycaenid tribe Theclini (obl: obligate myrmecophiles, fac: facultative myrmecophiles, phil: all myrmecophiles, xen: myrmecoxenous species). Given are absolute species numbers (database see Appendix). P: probability of Chi² statistics for 2x2 contingency tables.

RI	1—3	4/5	P
obl	21	9	0.755
fac	29	9	
phil	50	18	0.047
xen	39	4	

hostplants	Fabales	other plants	P
obl	9	21	0.58
fac	8	30	
phil	17	51	0.001
xen	0	43	

hostplants	Fabales + Santalales	other plants	P
obl	13	17	0.592
fac	19	19	
phil	32	36	< 0.001
xen	0	43	

reported are facultative and rather loose (*Amblypodia anita* is stated to have no ant-associations despite its ant-organs: Bell 1915). All species are oligophagous and do neither feed on legumes nor on mistletoes, but show a preference for young plant tissue.

Loxuriti

The Loxuriti contain nearly 60 species (information available for 11 species) and are subdivided in three groups (treated as subtribes in Scott & Wright 1990). Two of these have characteristic hostplant preferences, the *Loxura* group feeding on young growth of monocots (Dioscoreaceae, Smilacaceae), whereas the *Cheritra* group mainly utilizes young growth of Fabales (but also Rubiaceae, Myrtaceae and Lauraceae). The *Horaga* group has hostplant records from Euphorbiaceae, Coriariaceae, Myrtaceae, Styraca-ceae, Rubiaceae, and Sapindaceae. As a whole, Loxuriti utilize 12 hostplant families and are rather polyphagous (RI = 3.18 ± 1.40, FI = 2.18 ± 1.47, n = 11).

Loxuriti larvae are usually myrmecophilous, although information regarding myrmecophily in *Horaga* and *Rathinda* is missing. *Cheritra freija* is polyphagous on young growth including legumes, but is myrmecoxenous in contrast to the predicitions of the preference and host range hypothesis. Species of the *Loxura* group are oligophagous, but ant-associated. Hence, the limited information available for this sub-

tribe does not support any of both hypotheses, but indicates that taxon-characteristic hostplant relationships and a basic preference for young plant growth are prevalent.

Iolaiti

The hostplant relationships within this subtribe are astonishingly monotonous (RI = 2.22 ± 0.73, FI = 1.06 ± 0.24). All 64 species for which information is available live on Loranthaceae or on the closely related Olacaceae (6 species). Single deviating records (e.g. Verbenaceae for *Tajuria diaeus*) most likely refer to the host trees on which the true hostplants (mistletoes) grow.

However, ant-associations are seemingly not very strongly developed, and sure records exist for only eight species. Several of these are stated to be just very occasionally attended by ants (e.g. Bell 1915). In a number of species the presence of larval ant-organs has been denied, albeit the records are partially controversial. Though more ant-associations will almost certainly be detected if the arboricolous Iolaiti larvae will receive a closer study in the field (especially the species where ant-organs are undoubtedly present), the morphological and behavioural observations strongly suggest that myrmecophily is rather weakly developed among the Iolaiti.

This sharply contrasts to the preference hypothesis (mistletoe-feeders are expected to show a high degree of myrmecophily), and the host range hypothesis does not apply to this oligophagous subtribe at all.

Remelaniti

Nothing is known concerning the larval biology of this small group (seven species) except hostplant records for two species (Loranthaceae, Ericaceae, Hypericaceae, Myrsinaceae), and any discussion must await further information.

Hypolycaeniti

This Afro-Oriental subtribe consists of two genera (sensu lato) with characteristic larval nutrition (information available for 11 of c. 55 species). The African genus *Leptomyrina* feeds inside the leaves of succulent plants in arid regions (mainly Crassulaceae, also Aizoaceae). *Hypolycaena* caterpillars are basically polyphagous with a distinct predilection of young foliage and inflorescences, but three species are specialists solely feeding upon Orchidaceae flowers.

As a whole, Hypolycaeniti larvae are polyphagous (RI = 3.73 ± 0.79, FI = 2.81 ± 3.12, n = 11) and utilize 19 hostplant families with no predilection of legumes or mistletoes.

All species are supposedly myrmecophilous irrespective of their host ranges or preferences. Two Oriental species (*Hypolycaena phorbas, H. erylus*) are probably obligate myrmecophiles with a very wide host range and could thus be seen as examples of amplified host ranges in response to specific myrmecophily. However, another African species (*H. philippus*) is likewise extremely polyphagous (at least eight

hostplant families), but is unspecifically associated with ants from two subfamilies. So, neither the host range nor the preference hypothesis are generally valid for the larvae of Hypolycaeniti.

Deudorigiti

The larvae of this largely Afro-Oriental subtribe (information available for 46 out of c. 200 species) utilize at least 31 plant families as hosts with a distinctive preference for legumes (recorded for 26 species). Other important hostplants belong to the Sapindaceae, Rosaceae and Myrtaceae (8 species each), Proteaceae (7 species), and Rubiaceae (6 species). Mistletoes play almost no role as larval hosts. Practically all Deudorigiti larvae preferentially or exclusively feed on particularly nutritive plant tissues like young foliage, flowers or ripening seeds.

Facultative myrmecophily is widespread among the Deudorigiti, but reductions occur in some groups with larvae feeding inside flowers or fruits (*Bindahara, Capys*, some *Deudorix* species). There is a significant relationship between hostplant preference and myrmecophily (Tab.8): reductions of myrmecophily are unknown from species feeding on legumes.

As a whole, Deudorigiti larvae are rather polyphagous (RI = 2.82 ± 1.51, FI = 2.57 ± 2.72, n = 44), although the majority of species is known from only one hostplant family. However, myrmecoxeny is known exclusively among food specialists, whereas truly polyphagous species are generally associated with ants, resulting in a significant relationship between polyphagy and myrmecophily. Hence, both the preference and the host range hypothesis are supported by evidence from the subtribe Deudorigiti.

Eumaeiti

Biological information on this most diverse of all lycaenid subtribes is still rather scanty and only allows a tentative discussion. In the following analysis 221 species are considered including a bulk of unpublished data on Neotropical species kindly communicated by Robbins (these are not given in the Appendix).

Eumaeiti hostplant records cover no less than 90 plant families. With 56 entries legumes are mentioned most often, followed by Rosaceae (20 species), Fagaceae (17), Solanaceae (13), Sapindaceae, Euphorbiaceae, Loranthaceae, Asteraceae (12), Polygonaceae (11), and Rhamnaceae and Verbenaceae (10). Unusual lycaenid hostplants are cycads (5 species), conifers (11), or monocots (14). Families not known to serve as lycaenid hosts outside the Eumaeiti are Cactaceae, Apocynaceae and Asclepiadaceae. The larvae of at least one species are even predators of Homoptera (Boulard 1986).

In all, the available data are indicative of a highly diverse pattern of hostplant use, although several genera or species groups exhibit taxon-specific hostplant preferences (e.g. *Eumaeus* on cycads, *Allosmaitia* on Malpighiaceae, *Atlides* on Loranthaceae, *Arawacus* on Solanaceae). Legumes are recorded for only one quarter of the Eumaeiti species documented. Most Eumaeiti larvae typically feed on young growth, inflorescences or fruits, many of them even have endophytic life-habits.

Tab.8: Host range (range index RI 1—3 versus 4/5), association with legumes, and myrmecophily in the lycaenid subtribe Deudorigiti (phil: myrmecophiles, xen: myrmecoxenous species). Given are absolute species numbers (only 33 species are considered where a reasonable assignment regarding larval ant-associations is yet possible [see Appendix]; a separate analysis based on tentative assignments for some *Deudorix* species [total n = 45] yielded identical statistical results). Test statistics for 2x2 contingency tables: Fisher's exact probability (P).

RI	1—3	4/5	P
phil	14	12	0.027
xen	7	0	

hostplants	Fabales	other plants	P
phil	22	4	< 0.001
xen	0	7	

Since data on ant-associations of Eumaeiti immatures are exceedingly fragmentary, only some features shall be mentioned here. A thorough analysis must be deferred. Only four of the recorded 26 myrmecophilous species, and only 13 of the supposed 51 myrmecophiles (a low conservative estimate) feed on legumes, the respective figures for mistletoes being one and five species (these figures only concern the species with information available). Thus, the preference hypothesis appears to be invalid for Eumaeiti larvae.

On average, the host range of Eumaeiti caterpillars is moderate (RI = 2.63 ± 1.39, FI = 1.97 ± 2.86, n = 211). However, a number of species is highly polyphagous, *Strymon melinus* being recorded from more than 30 plant families (possibly the most polyphagous butterfly species in the world). Twenty-six polyphagous species with RI = 5 (i.e. with three or more hostplant families) have not yet been recorded to be attended by ants, whereas only 8 of 26 known myrmecophiles (and 11 of 51 presumed myrmecophiles) utilize two or more hostplant families.

Hence, there is no evidence for amplified host ranges among ant-associated Eumaeiti larvae. Rather, highly polyphagous Eumaeiti species (that are all specialized flower- or fruit-feeders) tend to be weakly myrmecophilous or myrmecoxenous.

The patterns of hostplant use and myrmecophily of the two sister-groups Deudorigiti and Eumaeiti differ remarkably. The widespread use of legumes and inflorescences as larval food in both subtribes suggests that the presumably myrmecophilous larvae of their common ancestor also fed on such plant parts. Deudorigiti larvae mostly retained myrmecophily as well as the predilection of legumes and nutritive plant parts. Eumaeiti larvae still predilect protein-rich plant tissues, but their preference for legumes is low, the range of utilized hostplant taxa has been enormously amplified, and polyphagy is often correlated with reductions of myrmecophily.

An overall discussion of Eumaeini hostplant relationships and its possible trade-offs with myrmecophily is yet impossible given the meagre database for Neotropical Eumaeiti. Even an analysis restricted to the Old World subtribes must remain un-

satisfactory since information on ant-associations of Iolaiti and Deudorigiti is very incomplete.

A tentative calculation based on 90 Old World species, for which a reasonable assignment of the degree of myrmecophily is currently possible (i.e. omitting several African *Iolaus* and *Deudorix* species), yields significant relationships between myrmecophily and the preference for legumes (Chi² = 6.31), or between ant-association and host range (Chi² = 4.01, p < 0.05 for both). Given the taxonomic heterogeneity of the subtribes considered, and in view of the questionable monophyly of the Eumaeini as a whole, these statistical results must be viewed with great caution.

Polyommatini

Candaliditi

This Austro-Melanesian subtribe has a very heterogeneous hostplant pattern (RI = 3.38 ± 1.39, FI = 2.23 ± 1.63, n = 13). Eighteen families have been recorded. A general preference is not apparent. Five species utilize Lauraceae, while only two feed on legumes.

Ant-associations are known or suspected from the majority of species, irrespective of the hostplant taxa and the width of the host range. One species stated to lack ant-associations (*Adaluma urumelia*) feeds on Rutaceae. There is no evidence that the hostplant use of Candaliditi larvae follows the predictions of the preference or host range hypothesis.

Lycaenesthiti

Lycaenesthiti caterpillars have been recorded from 20 hostplant families and are on average rather polyphagous (RI = 3.12 ± 1.30, FI = 2.29 ± 2.16, n = 24). They exhibit a pronounced preference for legumes (16 species) as well as for young growth and inflorescences. Some of the obligate myrmecophiles have an amplified host range (e.g. *Anthene emolus*: Fiedler & Maschwitz 1989b), while others are food specialists. In all, the hostplant relationships of Lycaenesthiti clearly support both the preference and host range hypothesis.

Niphanditi

The only species with well-documented life-history feeds on Fagaceae and is obligatorily myrmecophilous, but this isolated information precludes further interpretations.

Polyommatiti

The larvae of this large subtribe utilize hostplants in at least 70 families. Nevertheless, distinct patterns are apparent. Legumes are highly preferred (157 species), followed by Lamiaceae (34), Rhamnaceae (24), Geraniaceae (17), Sapindaceae (15), Polygonaceae and Selaginaceae (14), and Rosaceae (12). Mistletoes are rarely used as hosts (two species).

On the genus or species group level, further very characteristic hostplant relationships can be observed (e.g. *Lepidochrysops* and *Pseudophilotes* on Lamiaceae, subgenera *Aricia* and *Agriades* of *Polyommatus* on Geraniaceae and Primulaceae respectively, the *Castalius* section on Rhamnaceae), but a more detailed analysis is beyond the scope of the present study. On average, most Polyommatiti larvae are oligophagous (RI = 2.57 ± 1.14, FI = 1.46 ± 1.47, n = 311).

A statistical analysis of the relationships between myrmecophily and hostplant use in the whole tribe Polyommatini yields interesting results. Myrmecoxenous Polyommatini significantly less often feed on legumes than their myrmecophilous relatives.

However, when comparing obligate and facultative myrmecophiles, the reverse result is highly significant: only very few obligatorily ant-associated Polyommatini use legumes as larval hosts (Tab.9). Furthermore, nearly half of the ant-associated species do not feed on legumes. Thus, it is questionable whether the predilection of legumes among Polyommatini larvae is really connected with myrmecophily (see below).

With regard to the host range, no significant differences between facultative and obligatory myrmecophiles, or between myrmecophilous and myrmecoxenous species can be found. In all these categories among the Polyommatini, less than 25 % of the species are truly polyphagous. So, even obligatorily ant-associated species, where ant-dependent oviposition is expected to occur, are mostly restricted to a single hostplant family or even genus.

Conclusions

General patterns of hostplant use within the Lycaenidae

As all other species-rich Lepidoptera families, the Lycaenidae utilize a diverse hostplant spectrum with records available from at least 144 plant families (Tab.18 in the Appendix; Ehrlich & Raven [1964] mention only 85 families for Lycaenidae and Riodinidae together).

However, 77 families have yet been recorded as hosts for three or less lycaenid species and are thus considered to be exceptional host taxa, either used only by a few food specialists, or serving as occasional hosts of polyphagous caterpillars. 35 families are utilized by 10 or more species and can hence be considered to constitute the main hostplant taxa of the Lycaenidae.

The taxonomically widespread connection with legumes (especially Curetinae, Aphnaeini, Zesiiti, Deudorigiti, Polyommatini) supports the assumption that Fabales were the hostplants of ancestral Lycaenidae. However, this hypothesis needs a careful inspection, based on a thorough outgroup comparison and a more complete knowledge of Poritiini hostplants.

Available hostplant data on the oldest lineages of the Nymphalidae (Libytheinae: Ulmaceae) and Riodinidae (Hamearinae: Myrsinaceae and Primulaceae; Harvey 1987) do neither support nor contradict an ancestral Lycaenidae-Fabales connection.

Tab.9: Host range (range index RI 1—3 versus 4/5), association with legumes, and myrmecophily in the lycaenid tribe Polyommatini (obl: obligate myrmecophiles, fac: facultative myrmecophiles, phil: all myrmecophiles, xen: myrmecoxenous species). Given are absolute species numbers (database see Appendix). P: probability of Chi² statistics for 2x2 contingency tables.

RI	1—3	4/5	P
obl	43	11	0.67
fac	200	60	
phil	243	71	0.68
xen	31	5	

hostplants	Fabales	other plants	P
obl	7	47	0.001
fac	161	99	
phil	168	146	0.001
xen	8	28	

Scott (1985) has even suggested that legumes were the ancestral hosts of the Papilionoidea as a whole, and this view is substantiated by the widespred use of Fabales as hosts in those subfamilies of most butterfly families retaining a number of plesiomorphic character states (Hesperiidae-Pyrginae, Papilionidae-Baroniinae, Pieridae-Dismorphiinae and Coliadinae: Scott & Wright 1990).

Again, however, an outgroup comparison yields no decision: the larvae of Hedylidae, the sister-family of the butterflies, are hitherto reported from Sterculiaceae, Malvaceae, and Euphorbiaceae (Scoble 1990).

Legumes by far lead the list of lycaenid hostplant records with entries for 322 species (questionable records omitted), but notably these are less than one third of the lycaenid species for which life-history information is available. Thus, even if nitrogen-fixing legumes are the most widespread, and presumably the ancestral, hostplants of caterpillars of the family Lycaenidae, they probably serve as hosts for less than 40 % of the extant species.

Other plant families of the subclass Rosidae that are well represented in the lycaenid hostplant list include: Loranthaceae (100), Sapindaceae (55), Rosaceae (49), Rhamnaceae (43), Euphorbiaceae (37), Myrtaceae (29), Combretaceae (27), Zygophyllaceae (21), Anacardiaceae and Crassulaceae (19), Geraniaceae (18), Proteaceae (15), and Malpighiaceae (12).

In all, plants out of at least 47 Rosidae families are utilized as hosts by larvae of 652 lycaenid species, and this subclass is hence by far the predominant hostplant group. However, the Aralianae families with their characteristic resins or ethereal oils are only very weakly represented.

The second important angiosperm subclass containing the hostplants of at least 137 lycaenid species are the Lamiidae. Important families are Lamiaceae (37) and the closely

related Selaginaceae (14), Verbenaceae (29), and Bignoniaceae (11) in the Scrophularianae, Solanaceae (15) and Boraginaceae (13) in the Solananae, and Rubiaceae (18) and Oleaceae (12) in the Gentiananae, whereas most Gentiananae families with their characteristic toxic alkaloids, such as Apocynaceae, Asclepiadaceae, or Loganiaceae, only exceptionally serve as hosts for lycaenid caterpillars.

Plant species of the Hamamelididae (here treated after Ehrendorfer 1983, i.e. including the Urticales often transferred to the Dilleniidae) are fed upon by 74 lycaenids (Fagaceae [48 species], Moraceae [12], Ulmaceae [10], and eight further families). Among the Caryophyllidae families only the Polygonaceae are utilized by a larger number of lycaenids (58 species), while nine further families together house only 17 species. Remarkably, Polygonaceae lack the typical caryophyllid secondary compounds (betalaines).

Plants belonging to 26 families of the subclass Dilleniidae are fed upon by 83 lycaenid species with Ericaceae (19 species), Sterculiaceae (18), Malvaceae (10), Sapotaceae (9) and Cistaceae (8) as relatively important families. The primitive angiosperm taxa Magnoliidae (Lauraceae, Annonaceae, Piperaceae; together 17 species) and Ranunculidae (Ranunculaceae, two species) are rarely used as hosts, as are the highly advanced Asteridae (27 species on Asteraceae, but hardly any of these is specialized upon Asteraceae).

Monocots of 17 families are utilized by 36 species with Dioscoreaceae (10) and Bromeliaceae (8) prevailing, but only few of these are true monocot specialists. Rather unusual hostplants among the Lycaenidae and the butterflies as a whole are conifers (12), cycads (8), and ferns (2). The feeding habits of Liptenini (58 species feeding on lichen) and Miletinae (37 aphytophagous species) have already been discussed in detail.

Concerning the architecture of lycaenid hostplants, woody plants (trees and shrubs) and epiphytes (mistletoes) are distinctly dominant, while herbaceous plants are only utilized to some extent by the temperate zone Polyommatiti.

In all, while the subfamilies Poritiinae and Miletinae have considerably aberrant feeding habits, the hostplant pattern of the subfamilies Curetinae and Lycaeninae can be characterized by a presumably ancestral and widespread connection with Fabales and some other Rosidae families, with limited extensions towards Fagales, Urticales, Polygonales, Malvales, Ericales, and some Lamiidae groups (mainly Lamiales). Other plant taxa constitute only exceptional or occasional hosts.

The often claimed predilection of young growth and inflorescences (e.g. Pierce 1984) is well developed in the Curetinae, some Theclini subtribes, the Eumaeini and Polyommatini, but is less pronounced in the Aphnaeini and Lycaenini. Overall, this predilection of highly nutritive plant parts may thus well constitute a basic character of lycaenid hostplant use, but unfortunately this trait has been recorded rather incompletely.

An important corollary of these results is that certain plant taxa, albeit extremely diverse, rarely or never serve as hosts for lycaenid caterpillars. Such distinctly underrepresented plant taxa are Asteraceae and Orchidaceae (which are the by far largest angiosperm families in the world), further Caryophyllales, Aralianae, Theanae,

Violanae, Apocynaceae, Asclepiadaceae, Scrophulariaceae, Acanthaceae, Gesneriaceae, and all monocots. Families like Aristolochiaceae, Caryophyllaceae, Violaceae, Passifloraceae, Brassicaceae, Dipsacaceae, Campanulaceae, Cyperaceae and Juncaceae are totally absent from the current lycaenid hostplant list.

Apparently, the Lycaenidae with their specialization towards the Rosidae had limited success in colonizing these latter plant groups that are mostly characterized by peculiar secondary compounds. Although direct evidence is missing, this suggests that chemical barriers have played a major role in the evolution of hostplant relationships within the Lycaenidae. Host shifts occurred most often among taxonomically or chemically related plants, or while specializing on plant tissues rather poor in secondary compounds (e.g. young unexpanded foliage).

Indeed, polyphagy of many lycaenids is strongly correlated with specialization on young foliage or inflorescences, suggesting that "oviposition errors" under such circumstances provided important opportunities for amplifying the host range (Chew & Robbins 1984). Harvey (1987) noted a similar trend towards polyphagy in Riodinidae caterpillars utilizing extrafloral plant nectar.

This generalized view of Lycaenidae hostplant relationships is partly obscured by the characteristic and highly diverse hostplant relationships of many of the subordinated taxa (see above). Most likely this is due to adaptations of these taxa to cope with the secondary compounds of their respective hostplants.

In this respect the lycaenids are typical herbivores and pronouncedly resemble the butterfly families Papilionidae, Pieridae and Nymphalidae, where typically subfamilies, tribes or genus-groups all share basic hostplants, although numerous secondary deviations do occur (e.g. Ackery 1988). A general reservation of the patterns described here is that the available database considers only one fourth of the extant species diversity of the Lycaenidae.

Lycaenid hostplants in comparison to other butterflies

Ehrlich & Raven (1964) have already noted that the hostplant ranges of Nymphalidae and Lycaenidae apparently show little overlap. On the grounds of Ackery's recent treatise (1988) and the data compiled in the Appendix, this notion can now be investigated more precisely.

Nymphalids indeed heavily utilize plant taxa that play little or no role as lycaenid hosts. Monocots (mainly Bromeliales, Cyperales, Poales, Arecales) are the typical hosts of Brassolinae, Amathusiinae, Satyrinae, and several Morphinae. Acraeinae predominantly feed on Violanae and Urticales; Heliconiinae on Passifloraceae; Argynninae on Violales; Melitaeinae on Scrophulariaceae and Asteraceae; Nymphalinae, Apaturinae and Libytheinae on Urticales; Danainae on Asclepiadaceae and Apocynaceae; and Ithomiinae on Solanaceae.

Only some *Morpho* species and, in part, the subfamilies Charaxinae and Limenitinae show some overlap with the Fabales or, more generalized, with the Rosidae theme so typical for the Lycaeninae.

This gross pattern provokes an evolutionary interpretation, and I here present two ideas that may stimulate, but not anticipate, a more detailed discussion. First, the general Rosidae theme of the Lycaeninae could indicate that these butterflies and the Rosidae diversified in parallel. The Rosidae are an assemblage of moderately advanced dicots that mainly evolved during the late Cretaceous and early Tertiary, and from zoogeographical reasons the principle divisions of the Lycaenidae occurred in this same period.

In this scenario, the Lycaenidae basically maintained and diversified while pertaining their primary association with Rosidae families (notably legumes). They only sporadically managed to shift to unrelated lineages, most likely in the presence of chemical similarities. This "parallelism in time scenario" could explain why lycaenids do rarely feed on either ancestral (Magnoliidae) or advanced angiosperms (Asteridae, many monocots).

A second and by no means mutually exclusive scenario invokes competition. Nymphalids, starting from their possibly primary association with Urticales (Libytheinae, Nymphalinae), successfully colonized the modern angiosperm taxa (Dilleniidae, Lamiidae, Asteridae, monocots) and occupied many potential niches for butterfly caterpillars, thus preventing a more extensive shift of lycaenids onto these plants. This "competition scenario" implies that nymphalids have derived their remarkable diversity through considerably effective mechanisms to cross the chemical barriers imposed by secondary plant compounds.

A comparison of Papilionidae hostplants with the lycaenid pattern likewise yields distinct differences. Papilionids heavily utilize Magnoliidae (e.g. Lauraceae, Annonaceae, Aristolochiaceae), suggesting an ancient association with primitive angiosperms. This well matches the systematic position of the Papilionidae as the most primitive family of true butterflies. The basic radiation of papilionids certainly predates that of lycaenids.

Furthermore, advanced Papilioninae (*Papilio* in part) have specialized on resiniferous plants (Rutaceae, Apiaceae). Both the ancient and the more modern papilionid hostplant groups bear little importance for caterpillars of the Lycaenidae. An interpretation of the association of the primitive monobasic papilionid subfamily Baroniinae with legumes is currently impossible.

Pieridae larvae feed on legumes and other Rosidae (Loranthaceae, Rhamnaceae: Dismorphiinae, Coliadinae), as well as on Capparales (many advanced Pierinae). The latter plants contain highly characteristic secondary compounds (glucosinolates etc.) and have never been reported to be utilized by lycaenid caterpillars.

The considerable overlap of ancestral Pieridae and Lycaenidae hostplants suggests that their last common ancestor might have lived on legumes. Possibly, the basic radiations of Pieridae and Lycaenidae occurred at the same time ("parallelism in time scenario"), with one pierid group later successfully colonizing a novel type of hostplants.

The hostplants of Riodinidae are rather sketchily known and cover a broad array of at least 46 dicot and monocot families (Harvey 1987). A general pattern is not yet ap-

parent, although several subfamilies or tribes have characteristic hostplant relationships. Riodinid caterpillars do not predilect young foliage or inflorescences of their hostplants, thus differing distinctly from many lycaenids.

In summary, confirming the view of Ehrlich & Raven (1964), there is only limited overlap in the patterns of hostplant use between the Lycaenidae, and the remaining butterfly families Papilionidae, Pieridae, Nymphalidae and Riodinidae. The only significant congruence between the pierid subfamilies Dismorphiinae and Coliadinae, and Lycaenidae suggests a common ancestral association of these two families with the Rosidae and especially with legumes.

The characteristic differences among the hostplant patterns of the butterfly families can be tentatively related to historical coincidences of major steps in angiosperm evolution with basic radiations of the respective butterfly taxa, as well as to sequences of occupation of potentially available hostplant taxa. Clearly, these topics requires a more thorough analysis beyond the scope of the present study.

Are there trade-offs with myrmecophily?

In the preceding paragraphs three generalized results have crystallized out: not surprisingly, most lycaenid subfamilies, tribes or subtribes possess taxon-characteristic hostplant-relationships; there is indeed an overall association of phytophagous lycaenids with the plant subclass Rosidae and especially the order Fabales, as well as a predilection for young foliage or inflorescences; and, the hostplant pattern of Lycaenidae shows only limited overlap with the remaining butterfly families. These findings shall now be related to myrmecophily.

At first glance the overall lycaenid pattern appears to support the "preference hypothesis", according to which myrmecophilous lycaenids should preferably feed on protein-rich plants such as Fabales or Santalales (Pierce 1985). However, several objections qualify this view.

First, legumes appear to be the ancestral hostplants of the Lycaenidae and are fed upon by the primarily myrmecoxenous Curetinae as well as by rather old Pieridae lineages. In the latter family, there are no certain records of true myrmecophily, and the few reports of ants visiting the secretory setae of young pierid caterpillars predominantly involve species feeding on non-legumes (e.g. Brassicaceae).

Secondly, within the myrmecophilous subfamily Lycaeninae the connection with legumes is widespread, but by no means ubiquitous. Myrmecophilous taxa like Luciiti, Arhopaliti, Catapaecilmatiti, Amblypodiiti, Loxuriti and Hypolycaeniti show only very weak associations with Fabales or Santalales at most.

Thirdly, even in such taxa with a general Fabales theme (Aphnaeini, Zesiiti, Deudorigiti, Eumaeiti, Polyommatini) a considerable portion of the myrmecophiles does not utilize legumes as larval food (e.g. 48 % in the Aphnaeini, 46.5 % in the Polyommatini).

Fourthly, mistletoe-feeders generally do not show a pronounced state of myrmecophily. While the few Ogyriti species are all myrmecophilous, the by far more species-rich Iolaiti apparently exhibit a lower level of myrmecophily, and ant-associations are

unknown from several mistletoe-feeders in other taxa (Eumaeiti: *Atlides, Callophrys*). In all, only about one half of the ant-associated Lycaenidae caterpillars feed on legumes or mistletoes, while the other half utilize a broad range of plants including ferns, cycads, or monocots.

Furthermore, there is no indication that obligatorily myrmecophilous lycaenids show a more close association with legumes than their facultatively ant-associated counterparts. If legumes were really that important for maintaining ant-associations, one should expect that obligatory myrmecophiles do pronouncedly predilect these plants. Within the Aphnaeini, however, the proportions of legume-feeders among obligate and facultative myrmecophiles are nearly identical, and within the Polyommatini the pattern is even reversed. In this tribe the majority of obligate myrmecophiles do not feed on legumes.

Finally, nitrogen-fixation is not restricted to the Fabales, but occurs in several families of the Hamamelididae (Betulaceae, Myricaceae, Casuarinaceae), Rosidae (Rosaceae, Rhamnaceae, Coriariaceae, Elaeagnaceae), and Dilleniidae (Ericaceae), always by means of symbioses with actinomycete fungi (Ehrendorfer 1983).

All these families are found in the hostplant list of lycaenid caterpillars, but only from three of the 13 lycaenid species, that reportedly feed on the genera known to have such fungus-symbioses, ant-associations have been recorded (*Hypochrysops piceatus, Celastrina argiolus, Lycaeides idas*).

These objections do not truly invalidate the preference hypothesis in total. In fact, it is well conceivable that the association of ancestral Lycaeninae with legumes provided an important nutritional preadaptation for these butterflies to enter into mutualistic associations with ants based on trophic secretions.

Experimental evidence also supports the notion that the quality of larval nutrition may be decisive for the maintenance of myrmecophily (Fiedler 1990c, Baylis & Pierce 1991). Rather, the above arguments indicate that starting from their primary association with legumes, roughly one half of the myrmecophilous lycaenids have successfully increased or even entirely shifted their hostplant range, but still maintain their symbiotic relationships towards ants.

Obviously, myrmecophilous lycaenid caterpillars were able to specialize on novel hostplants in evolutionary time, and, given the large diversity of hostplants of myrmecophilous lycaenids, there is no evidence that ant-associations have provided a powerful selective force preventing or channelling hostplant shifts.

In one respect, however, the preference hypothesis generally holds true: secondary myrmecoxeny is much more common in species not feeding on legumes, this difference being statistically significant in the Theclini, Deudorigiti, and Polyommatini. Thus, shifts towards "nutritionally inferior" hostplants enhance the likelihood of reducing ant-associations, whereas on legumes the ecological conditions have more rarely favoured the step towards secondary myrmecoxeny (see last chapter).

The second hypothesis concerning lycaenid hostplant patterns and myrmecophily predicts an amplified host range in response to associations with specific ants (Pierce

& Elgar 1985). Based on the results presented above, this trait is extremely instable across the higher lycaenid taxa.

Among the well-known Aphnaeini and Polyommatini there is no indication that myrmecophiles have a wider host range than myrmecoxenous species, or that obligate myrmecophiles are more polyphagous than facultative ones. Overall, 75 % of the Aphnaeini and Polyommatini are oligophagous (i.e. restricted to one hostplant family) with no respect of their degree of myrmecophily.

In contrast, there is a statistically significant difference in the degree of polyphagy between myrmecophiles and non-myrmecophiles within the Theclini and Eumaeini. The majority of polyphagous Theclini (a similar result was obtained for the Luciiti alone) are usually myrmecophilous, as are polyphagous members of Old World Eumaeini tribes (this trend is particularly prevalent in the Deudorigiti). In contrast, most myrmecoxenous Theclini and Eumaeini species are food specialists. Astonishingly, the degree of polyphagy does not differ between obligatory and facultative myrmecophiles among the Theclini (same result obtained for Luciiti alone), and within the Old World Eumaeini obligate and specific myrmecophiles are almost unknown.

Hence, it is very unlikely that the polyphagy of quite a number of Theclini and Eumaeini caterpillars has evolved in response to specific ant-associations. If this were the case, the widest host ranges were to be expected among those lycaenids obligatorily associated with particular host ants. This does clearly not apply to the Deudorigiti, at least.

Furthermore, less than 25 % of the species of both tribes are reportedly polyphagous. So, polyphagy in the Theclini and Eumaeini may only in single instances really be related to obligatory and specific ant-associations. Rather, the physiological potential to utilize a wide hostplant range (usually via flower or fruit-feeding) appears to be a characteristic trait of certain genera (e.g. *Hypochrysops, Arhopala, Hypolycaena, Deudorix, Rapala*), and only within groups thus phyletically preadapted the relative importance of ants as oviposition cue could secondarily override the generally leading role of plant chemistry (e.g. *Hypochrysops ignitus, H. miskini, H. apelles, Arhopala centaurus, A. pseudocentaurus, Hypolycaena phorbas, H. erylus*).

The relative over-representation of oligophagous species among myrmecoxenous Theclini might be due to the trend outlined above that myrmecoxeny is more likely to evolve on "nutritionally inferior" hostplants. Lauraceae, Moraceae (*Philiris*), Fagaceae and related Hamamelididae families (Thecliti) are rather untypical lycaenid hostplants whose colonization supposedly required appropriate physiological specializations.

At the same time these plants may well represent such inferior hostplants that, in concert with other ecological factors (e.g. low ant abundance in canopies of temperature zone Fagaceae forests), have favoured the reduction of ant-associations. In addition, oligophagous caterpillars are generally subject to a lower selective pressure arising from predation (Bernays 1988, Bernays & Cornelius 1989), and this alternative "defense" may further have limited the selective advantage of low-level myrmecophily.

Myrmecoxenous Eumaeini often exhibit another type of alternative defense, namely endophytism, which in combination with monophagy apparently furthered the reduction of myrmecophily (e.g. *Artipe eryx, Bindahara phocides, Capys*).

The myrmecoxenous genus *Eumaeus* even feeds on cycads containing toxic secondary compounds (e.g. cycasine), and its gregarious aposematic caterpillars have been shown to be unpalatable to ants and birds due to the sequestering of these allelochemicals (Bowers & Larin 1989, Bowers & Farley 1990).

In summary, the general hostplant pattern of lycaenid caterpillars seems to be governed by the same principles as in other Lepidoptera taxa: chemical barriers and adaptations to overcome these, availability of potential hostplants in space (i.e. geographic range) and time, and possibly competition and resource partitioning among the major butterfly lineages.

As a consequence, the hostplant pattern of the Lycaenidae shows distinct relationships to phylogeny and systematics, and the consideration of these relationships is crucial. There is little evidence for consistent trade-offs between hostplant preferences and myrmecophily across the whole diversity of the Lycaenidae, suggesting that in evolutionary time lycaenid caterpillars were able to maintain ant-associations even on unusual hostplants, and thus limiting the explanatory or predictive validity of the preference and the amplified host range hypothesis proposed by Pierce (1985) and Pierce & Elgar (1985), respectively.

Significant trade-offs do however exist between the evolution of secondary myrmecoxeny and the association with non-legume hostplants. A universal correlation between hostplant range and myrmecophily does not exist, and in the cases where ant-dependent oviposition coincides with polyphagy, this is usually based on rather catholic feeding habits of the whole taxonomic group in question.

ZOOGEOGRAPHY OF LYCAENID-ANT INTERACTIONS

Zoogeography of the Lycaenidae

Only one work (Pierce 1987) has previously dealt with the zoogeographical aspects of myrmecophily within the Lycaenidae. The main conclusion of Pierce was that myrmecophily is much more common in the southern hemisphere, with 70—90 % of all lycaenids being ant-associated, than in the northern hemisphere, where myrmecophily was stated to occur in less than one third of the species.

In addition, obligate ant-associations were found to be widespread in the southern hemisphere, whereas in the Holarctic region less than 10 % of the lycaenids are obligatorily myrmecophilous.

Thus, the proportion of myrmecophilous lycaenids and the obligateness of their ant-associations were postulated to show a clear north-south disparity. Pierce (1987) emphasized that this disparity should neither be due to any peculiarities in the distribution of myrmecophily among the lycaenid taxa, nor to the different geographical distributions of the lycaenid taxa themselves.

However, since in the preceding chapters significant interrelationships between lycaenid systematics, the larval hostplant patterns, and the occurrence and specificity of myrmecophilous associations have been disclosed, it seems worthwhile to search for such correlations between systematics, zoogeography, and myrmecophily as well.

Furthermore, the higher classification underlying the study of Pierce (1987) still contained, among others, the "Theclinae" sensu Eliot (1973), and these are now known to be a paraphyletic assemblage. The use of paraphyletic or polyphyletic units may well have masked important evolutionary traits.

In addition, the figures given by Pierce (1987) concerning the proportion of myrmecophilous lycaenids in the western Palaearctic region have recently been questioned on the grounds of an extensive literature survey (Fiedler 1991). Therefore, the whole complex of zoogeographical implications on myrmecophily will here be carefully re-examined within the systematic framework of the preceding chapters.

As a first step, the zoogeography of the higher lycaenid taxa has to be reviewed briefly. Eliot (1973) was the first to discuss the global zoogeography of the Lycaenidae using his systematic approach, and the reader is referred to his work for numerous further details and references (see also Stempffer 1967).

The main aim of this first part of the analysis is to investigate whether the higher lycaenid taxa have characteristic distributional patterns that may affect the faunal composition in the different zoogeographic regions. In the second part of this chapter, the systematic structure of the lycaenid faunas and their proportions of myrmecophilous species will be examined using 8 selected regions. Finally, I will attempt a synthesis of these data on systematics, zoogeography, and myrmecophily.

Poritiinae

This second-largest lycaenid subfamily is entirely restricted to the Old World tropics and subtropics. It further divides into two tribes with characteristic distributions. The Oriental Poritiini comprise about 50 species that occur solely in India, South East Asia and the Indonesian archipelago. The Ethiopian Liptenini with more than 500 species (Stempffer 1967), in contrast, are confined to Africa south of the Sahara desert with main diversity in tropical central Africa.

The Liptenini further subdivide into three subtribes one of which, viz. the Durbaniiti, is a small and basically southern African taxon of more xeric habitats (perhaps a specialized lineage derived from Lipteniti-like ancestors). The Pentiliti are distributed throughout Africa south of the Sahara with some 130 species, while the most advanced Lipteniti (more than 380 species) are mainly tropical.

There is evidence that the two Poritiinae tribes are sister-groups, although their evolutionary history is not well understood. Poritiinae larvae are basically myrmecoxenous, with only some Lipteniti exhibiting relationships towards ants that are supposed to represent commensalism. Nevertheless, the largely myrmecoxenous Liptenini account for a siginificant proportion (about 35 %) of the African lycaenid fauna. The Poritiini only weakly contribute to the diversity of the Oriental Lycaenidae (e.g. 6 % in Thailand, Peninsular Malaysia, and Borneo).

Miletinae

This rather small subfamily (about 140 species) is essentially confined to the Old World tropics as well, but it weakly extends into northern Australia, the eastern Palaearctic and the Nearctic region with one species each. The Australian and Japanese populations of *Liphyra brassolis* and *Taraka hamada*, respectively, have clearly secondarily invaded from South East Asia, which is the main distributional area of both species.

The Nearctic endemic *Feniseca tarquinius*, in contrast, may either represent an old Tertiary relic of a former Holarctic subtropical Miletinae fauna that was subsequently eradicated in the Palaearctic through the glaciations. Or, coming from eastern Asia, it may have entered America via the Bering strait. Anyway, the main stock of the Miletinae is clearly African and Oriental.

The two tribes Miletini and Liphyrini show a less sharp geographical disjunction than the two Poritiinae tribes. The Miletini are predominantly Oriental (about 75 species). Only the genera *Megalopalpus* (Miletiti) and *Spalgis* (Spalgiti) occur in Africa with less than 10 species together.

The Lachnocnemiti (included into the Miletini by Scott & Wright 1990, but more likely the sister-group of the Liphyrini: Eliot, pers. comm.) are entirely African (35 species), as are the Liphyrini (20 species) with the only exception of *Liphyra*.

The Miletinae everywhere constitute a minor component of the lycaenid fauna at most (8 % in southern Africa as well as in Thailand and Peninsular Malaysia, 11 % in Borneo).

Curetinae

The myrmecoxenous Curetinae (18 species) are confined to the Oriental region with one species extending into the eastern Palaearctic (*Curetis acuta*) and another occurring in New Guinea and adjacent archipelagos (*C. barsine*; Eliot 1990). Even in the area of their main diversity (Sundaland), the Curetinae do never build up more than 2 % of the lycaenid fauna.

Lycaeninae

This huge subfamily has a cosmopolitan distribution, but its tribes and subtribes again exhibit peculiar geographical patterns.

a) Aphnaeini

This tribe is basically confined to the Ethiopian realm. Only about a dozen species of the genus *Spindasis* occur in the Oriental region with a single representative extending as far northeast as Japan (*S. takanonis*).

Another and rather closely related lineage (*Cigaritis* including *Apharitis*), comprising a further dozen of species, is essentially eremic, reaching the southwestern Mediterranean area and extending through Arabia and the Middle East to the deserts of Central Asia.

The remaining 230 Aphnaeini species nearly exclusively occur in Africa south of the Sahara and constitute a significant component of the African lycaenid fauna (16 % of the whole African species diversity, but more than 36 % in southern Africa).

b) Lycaenini

This small tribe with less than 100 species provides a zoogeographical enigma (cf. Eliot 1973). The majority of species are Holarctic (genus *Lycaena* s. l.). A couple of *Lycaena* species occur in eastern Africa and have even reached South Africa, possibly having invaded through the East African mountains. Four additional *Lycaena* species are endemic to New Zealand, and their history remains a mystery.

The second phyletic lineage among the Lycaenini is the *Heliophorus* section, and this is largely an Oriental group with one genus (*Melanolycaena*) being confined to New Guinea (Sibatani 1974), while the single species of *Iophanus* is restricted to the mountains of Guatemala. The isolated occurrence of Lycaenini in New Zealand and Central America poses a challenge to zoogeography.

Irrespective of this, the largely myrmecoxenous Lycaenini contribute only 10-15 % to the species diversity of the Lycaenidae in the Holarctic realm and considerably less elsewhere.

c) Theclini

The Theclini sensu Scott & Wright (1990) are restricted to Eurasia and Australia with only 2 small Thecliti genera (*Habrodais, Hypaurotis*) occurring in North America. Two subtribes, Luciiti and Ogyriti, are entirely Austro-Melanesian (one Luciiti species, *Hypochrysops coelisparsus*, reaches South East Asia: Sands 1986). The third subtribe Zesiiti is also mainly Australian with the exception of the Indian *Zesius chrysomallus*.

The largest subtribe are the Oriental Arhopaliti with weak extension into New Guinea, northern Australia and the south-eastern Palaearctic. The fifth subtribe Thecliti is Sino-Oriental, but is also weakly represented in the western Palaearctic and Holarctic region and in South East Asia.

The basically myrmecophilous Theclini subtribes play major roles in the faunal composition of Australia (47 %) and South East Asia (ca. 30 %), while the largely myrmecoxenous Thecliti are important in the eastern Palaearctic region (e.g. 40 % in Japan). In all, the Theclini as a whole as well as its subtribes exhibit peculiar distributional patterns.

d) Eumaeini

This tribe is nearly cosmopolitan, but again its subtribes show very distinctive distributions. Catapaecilmatiti, Loxuriti, and Remelaniti (in the delimitations of the systematic chapter, see above) are strictly Oriental. Amblypodiiti, Iolaiti, Hypolycaeniti, and Deudorigiti are Oriental and African, Oxyliditi are African, and Hypothecliti are Papuan. There is some reason to assume that the Oriental members of the Iolaiti (and possibly those of the Hypolycaeniti and Deudorigiti as well) are derived from invaders from an old African stock (Eliot 1973).

The remaining and largest subtribe Eumaeiti is primarily Neotropical with only about 110 species in the Holarctic compared to an estimated 1000 species in the Neotropics (Bridges 1988, Robbins, pers. comm.). The North American Eumaeiti largely belong to the genera *Satyrium* and *Callophrys* s. l., and the Palaearctic representatives (ca. 55 species) are clearly derived from rather late invaders of the latter two genus groups via the Bering route.

e) Polyommatini

The Polyommatini are represented on all continents except Antarctica, but as with the Eumaeini their subgroups show distinctive patterns. Candaliditi are entirely Austro-Melanesian, Lycaenesthiti are African with weak secondary representation through the Oriental region including northern Australia, and Niphanditi are Oriental with one Palaearctic extension.

Polyommatiti are most strongly represented in Africa (*Cupidopsis, Uranothauma, Leptotes, Castalius, Zizeeria*, and *Euchrysops* sections are mainly African), the Oriental region (*Nacaduba, Jamides* and *Lycaenopsis* sections have their headquarters there), and the Palaearctic realm (*Everes, Glaucopsyche*, and *Polyommatus* sections).

The diversity of New World Polyommatini is surprisingly poor. The American members of the *Everes, Lycaenopsis, Glaucopsyche*, and *Polyommatus* sections are probably all derived from rather late invaders from Asia across the Bering route. Only the small aberrant *Hemiargus* group of genera within the *Polyommatus* section is truly American with less than 30 species (Nabokov 1945).

Eliot (1973) assumes that this *Hemiargus* group represents an earlier invasion across the Bering strait, and this agrees rather well with the today distribution of some of its members (cool-temperate mountainous Andine habitats). The isolated occurrence of

single members of the mainly African genera *Leptotes, Brephidium*, and *Zizula* is probably best explained by waif dispersal across the Atlantic ocean (Eliot 1973).

In summary, Africa and South Asia house the most diverse lycaenid faunas with respect to the presence of higher taxa (subfamilies, tribes, subtribes). The oldest lineages are today confined to the Old World tropics. The Palaearctic region has a comparatively depauperate fauna due to the repeated glaciations, and Australia's lycaenid fauna is rich in endemics (even on subtribal level), but rather poor in species diversity.

Most strikingly, the New World lycaenid fauna is very homogeneous. The Neotropical fauna consists almost entirely of members of one single subtribe, and the Nearctic fauna is largely derived from rather young Asian or Neotropical invaders. Apparently, the early and long-lasting isolation of North America precluded the evolution of a diverse autochthonous lycaenid fauna, and the Neotropics were primarily colonized by only one, albeit extremely speciose lineage, viz. Eumaeiti.

Obviously the distribution of the higher lycaenid taxa is far from being uniform, thus contradicting the conclusion of Pierce (1987) that the zoogeography of the Lycaenidae is largely independent of their phylogeny. In contrast, most higher lycaenid taxa as recognized throughout this work have distinctive distributions, and the systematic structure of the lycaenid faunas of all biogeographical realms investigated is indeed significantly shaped by these differences.

Since the higher taxa also have characteristic traits with regard to myrmecophily (see above), the faunal composition heavily influences the distribution and degree of myrmecophily in the various regions.

Zoogeographic patterns in lycaenid myrmecophily

Introductory remarks

In this chapter I will discuss the systematic structure, and the proportions of myrmecophilous species, of the lycaenid faunas of eight selected regions (viz. Europe and North West Africa, Japan, Australia, West Malaysia and Thailand, India, South Africa, North and South America). Except West Malaysia/Thailand and the Neotropics, these regions are the same as analysed by Pierce (1987), allowing direct comparisons with her data and conclusions.

From all of these regions, with the exception of the Neotropics, the faunistic knowledge of the Lycaenidae is sufficient to permit rather definite conclusions regarding approximate species diversity and systematic faunal structure. Despite the poor systematic and ecological knowledge, the Neotropics were included since they constitute a species-rich major biogeographical region for their own.

Therefore, all biogeographical realms are represented in the following analysis, although the Eastern Palaearctic and Neotropics strongly require a more thorough discussion on the grounds of more detailed faunistic and ecological information. The unevenness of the faunistic treatments and associated problems are discussed in the respective paragraphs.

Pierce (1987) performed comparisons between the regions using both the numbers of species and genera. Here I only focus on the analysis of species numbers on twofold reasons. First, as a theoretical argument, the species (as groups of populations maintaining genetic exchange) are the units that are subject to evolutionary processes such as selection or genetical drift.

Genera and higher taxa, in contrast, are historical entities at best (in the case of a truly phylogenetic system), or simply arbitrary assemblages (in the case of para- or polyphyletic taxa). Even monophyletic higher taxa are, however, not subject to ecological or evolutionary processes acting in phenomena like myrmecophily.

Accordingly, comparative analyses within higher taxa are appropriate to elucidate general trends and patterns of ecological phenomena like myrmecophily (see above), whereas simple numerical comparisons between higher taxa yield doubtful results, in particular when paraphyletic units are involved. At least, such quantitative analyses should incorporate the information content of the underlying hierarchical phylogenetic system (e.g. the concept of "taxic diversity": Vane-Wright et al. 1991).

Secondly, as a more practical argument, the use of lycaenid genera in any ecological and evolutionary considerations is precluded by the extremely uneven use of generic concepts among the different systematic approaches. This is mainly due to the preponderance of typological instead of phylogenetic systematics in the treatment of most butterfly groups.

Some examples may illustrate the associated difficulties. Higgins & Riley (1978) divided the European coppers (Lycaenini) into four genera (other authors even use seven genera). Kudrna (1986), in contrast, retained all these species in the single genus *Lycaena*. In North America, the coppers are likewise treated as one genus *Lycaena* by Scott (1986), whereas other authors subdivide the same group of 15 species into seven genera (Bridges 1988).

While *Lycaena* is probably a monophyletic taxon, most of the atomized "genera" are not based on synapomorphies, but simply reflect typological affinities. Furthermore, the exclusion of small, derived species-groups from larger, monophyletic genera often renders the remaining assemblage of species paraphyletic.

A parallel case is the generic treatment of the Holarctic *Polyommatus* group. Scott (1986) lumped all North American species into *Plebejus*, while Higgins & Riley (1978) splitted the European representatives into no less than 14 "genera".

Apart from all problems regarding the monophyly of the resulting taxa, it is obvious that such an unevenness must necessarily affect quantitative analyses based on different generic concepts. Pierce (1987), for example, used Higgins & Riley (1978) and Scott (1986) as taxonomic sources for Europe and North America, respectively. Thus, applying Scott's generic concept to the *Lycaena* and *Polyommatus* groups alone would have reduced the number of European lycaenid genera from 43 to 27. *Vice versa*, the result would be an increase of North America's genus number from 39 to at least 49.

Comparisons on genus level can only be useful if the generic concepts are harmonized, and this is at present impossible for the Lycaenidae fauna under a global view. Restric-

ting the following analyses to the species level still retains a number of unresolved tax-
onomic problems (species *versus* subspecies, sibling species etc.), but these seem more
tolerable for the purpose of this chapter.

The quantitative analyses were conducted in the following way. First the complete ly-
caenid fauna of each selected region (except the Neotropics) was assessed using
available faunistic literature, and rearranged according to the system used throughout
this work.

Secondly, all species occurring in one region, for whom ecological information is
available, were selected and the definite species records of myrmecophily were counted,
with obligate myrmecophily being treated separately wherever possible. Doing so, I
evaluated all information available for any species with no respect of the particular
geographic area in question (database see Tab.17 in the Appendix).

For example, *Leptotes pirithous* was designated as facultatively myrmecophilous using African
records in the analysis of Europe as well, although I have no European records of ant-associations
for this species. There is at present no published evidence that some populations of one lycaenid
species are myrmecophilous, while other populations of the same species are myrmecoxenous. Less
pronounced interpopulation differences in the degree or specificity of myrmecophily, however, are
likely to occur and are worth being documented.

This step of the analyses yielded the number of species with ecological information pre-
sent and its assured minimum proportion of facultative and obligate myrmecophiles
(the first three columns in the tables of the following paragraphs).

In a third step, the analyses were extended to the whole species diversity of the respec-
tive regions, using conservative myrmecophily estimates based on close relatives for all
those species where no definite information is available (the latter three columns in the
following tables).

This procedure is validated by the distinct correlations found between myrmecophily
and systematics (see above) as well as by the similarity of the results obtained for the
European fauna using this "indirect" method when compared with the direct evidence
(see below). The results of both approaches are then compared with those of Pierce
(1987).

Europe and North West Africa

The zoogeographical implications on myrmecophily in this part of the Western
Palaearctic have been discussed in detail by Fiedler (1991). Therefore, these results shall
be only briefly summarized here to facilitate further comparisons. The lycaenid fauna
of Europe and North West Africa (delimitations following Higgins & Riley 1978) is ta-
xonomically and ecologically rather well known, although for several species not even
the hostplants have been recorded.

Ecological data are present for the immatures of 107 species, 68 of which (63.5 %) are
surely known to be ant-associated including 10 (9.3 %) obligate myrmecophiles. The

whole fauna comprises 116 species (largely based on Kudrna 1986), of which an estimated 91 species (78.4 %) are most likely myrmecophilous including 10 (8.6 %) obligate myrmecophiles.

These figures contradict sharply to the results of Pierce (1987) who found a proportion of myrmecophiles of only 30.4 %. This difference has three main reasons. First, Pierce (1987) evaluated only a small list of references (largely the review papers of Hinton 1951, Malicky 1969b, and Kitching & Luke 1985, as well as identification guides such as Higgins & Riley 1978) and hence overlooked a number of records published in numerous faunistic or ecological reports.

Secondly, considerable progress has been made in recent years in the investigation of lycaenid myrmecophily in the Western Palaearctic, in particular in Spain and North West Africa (e.g. Munguira & Martín 1988, 1989a, b, Rojo de la Paz 1990). When compiling my database, I attempted to utilize all such sources exhaustively, including personal communications of several colleagues.

And thirdly, Pierce (1987) totally neglected the systematic component. Accordingly, she designated all species as "not myrmecophilous" in the absence of positive records. This procedure has been refuted in a number of cases where recent research has proven the existence of ant-associations, and it certainly results in a severe underestimate for the proportion of myrmecophiles in all other zoogeographical regions as well.

Given that at least more than 60 % (and most likely more than three quarters) of the European lycaenids are ant-associated, the question arises as to whether there is a systematic pattern involved. This is indeed the case.

In the Western Palaearctic, all lycaenids belong to the primarily myrmecophilous subfamily Lycaeninae, and the vast majority of species (72.4 %) are Polyommatini. In this latter group only very few species are definitely secondarily myrmecoxenous (six *Agriades* and *Vacciniina* species in the *Polyommatus* group). In addition, all of the five Aphnaeini species and seven of the European Eumaeiti species are certainly or most likely myrmecophilous.

Only the Lycaenini are a basically myrmecoxenous tribe with 13 representatives. Thus, the preponderance of one single myrmecophilous tribe alone accounts for the majority of myrmeophiles among the European lycaenids, whereas only one myrmecoxenous tribe comprises about one half of the rather few myrmecoxenous species.

Another interesting biogeographical result is a north-south gradient in the proportion of myrmecophilous species. Lycaenid species diversity increases distinctly from the North Cape towards the Mediterranean region and declines again towards the Sahara desert. The proportion of myrmecophilous species, in contrast, increases asymptotically from one third in the subarctic areas to roughly 80 % throughout the Mediterranean area and North Africa. South of 55 ° northern latitude the proportion of ant-associated species is consistently higher than 75 %, while only north of 65 ° this proportion is well below 60 %.

In other words: the proportion of myrmecophilous species does not differ substantially between the Mediterranean area and Central Europe. Pierce (1987) could not find a

Tab.10: Faunal composition and myrmecophily of European and North West African Lycaenidae (given are species numbers). The first 3 columns refer to species with life-history information and direct evidence for ant-associations present. The latter 3 columns are based on the myrmecophily estimates for the entire fauna (see text). n: total species number, phil: myrmecophilous, obl: obligatorily myrmecophilous.

Taxon	Species with information available			Entire fauna		
	n	phil	obl	n	phil	obl
Poritiinae	-	-	-	-	-	-
Miletinae	-	-	-	-	-	-
Curetinae	-	-	-	-	-	-
Lycaeninae	107	68	10	116	91	10
Aphnaeini	4	4	3	5	5	3
Lycaenini	10	0	0	13	0	0
Theclini	3	1	0	3	1	0
Eumaeini	11	6	0	11	7	0
Polyommatini	79	57	7	84	78	7
Lycaenidae	107	68	10	116	91	10

similar gradient between tropical and temperate areas in Australia, nor between subtropical and temperate areas of Japan. This suggests that climatic effects on myrmecophily become important only in high latitudes. In Europe, this obviously applies only to the northernmost boreal forests and the subarctic tundra.

At least three factors have probably shaped this gradient:

— First, the ant fauna of subarctic and northern boreal areas is extremely impoverished (Hölldobler & Wilson 1990, Heinze, pers. comm.). Thus, the chance of maintaining ant-associations and its related selective advantage is very low and, accordingly, myrmecophilous lycaenids have only the costs of developing ant-organs, but receive little, if any benefits.

— Secondly, the lack of appropriate ant partners may have limited or inhibited the recolonization of the subarctic region by myrmecophilous lycaenids after the glaciations.

— And thirdly, the short vegetation period in combination with limited nutritional resources may pose severe constraints to the production of energy-rich myrmecophilous secretions by lycaenid larvae.

A depauperate ant fauna and a shortened vegetation period are also characteristic for high altitude biomes. Interestingly, studies on altidudinal effects on Neotropical mutualisms between ants and plants (Koptur 1985) or membracids (Olmstead & Wood 1990b) revealed a distinct decrease of the number and proportion of ant-associations with increasing elevation. High-altitude membracids in South America are mostly not ant-associated, and plants bearing extrafloral nectaries may use alternative defense strategies there. Likewise, myrmecophily in the Neotropical Riodinidae is restricted to species of lower habitats (DeVries, pers. comm.).

Appropriate data for lycaenids are missing, but a preliminary survey of lycaenids in the Alps failed to detect significant differences in the altidudinal distribution of myrmecophilous versus myrmecoxenous lycaenids (Fiedler, unpublished). Detailed ecological studies on the degree of myrmecophily of species occurring at a wide range of altitudes would be rewarding. Furthermore, faunal surveys of mountain areas with a greater range of altitudes and a more diverse lycaenid fauna may demonstrate such altitudinal gradients in myrmecophily. At present, the available data are too scanty to allow appropriate analyses.

Overall, the lycaenid fauna of the Western Palaearctic is characterized by a high proportion of myrmecophilous species, a rather low number ($<$ 10 %) of obligate myrmecophiles, and the preponderance of one single myrmecophilous subtribe (Polyommatiti; see Fiedler 1991).

Japan

The lycaenid fauna of Japan comprises 61 species in three subfamilies. Due to the intensive work of numerous lepidopterists, the distribution and ecology of Japanese lycaenids is exceedingly well known. The life-histories of all species have been recorded, although a number of reports on larval biologies result from laboratory breedings only.

Accordingly, the knowledge of myrmecophily is still rather fragmentary. As a major source I utilized Shirôzu & Hara (1974), supplemented by a number of journal articles (e.g. Iwase 1953, 1954, 1955, Wakabayashi & Yoshizaki 1967, Ejima et al. 1978, Matsuoka 1978, Hama et al. 1989). For some species, information from outside Japan was used as well.

Twenty-seven of the 61 species (44.3 %) are surely known to be myrmecophilous, and seven further species are strongly suspected to be ant-associated as well. Thus, probably 55.4 % of the Japanese lycaenids are myrmecophilous. Only 5 or 6 species (8.2—9.8 %) maintain obligatory relationships to ants.

These figures again contrast distinctly with those given by Pierce (1987). However, the interpretation of her results is further complicated by inconsistencies within this latter paper. In her Tab.1, Pierce states that 14 out of 62 species (22.6 %) are myrmecophilous, while in Tab.2 and Figure 1, 25 out of 72 (!) species (34.7 %) are given as ant-associated. Reasons for the different total species numbers are not apparent (possibly a printer's error?), nor are the divergent myrmecophily data explained.

Given that the total species number of Japanese lycaenids is close to 61 (the status of some taxa is still a matter of debate — species or subspecies?), at least 44 %, but probably more than 50 % of the species are myrmecophilous.

There is again a distinct connection between faunal structure and myrmecophily. The 25 species of Japanese Polyommatini are probably all myrmecophilous, whereas in the Theclini myrmecophily is known only from three Arhopaliti species and one member of the Thecliti (*Shirozua jonasi*). The remaining 21 Thecliti species are apparently

secondarily myrmecoxenous, but due to their larval habits (most are living in the canopy of Fagaceae trees: Shirôzu 1962), ant-associations may have been partly overlooked.

The seven Eumaeini species contain few myrmecophiles (certainly documented for *Rapala arata* and *Satyrium w-album*, suspected for two further *Satyrium* species) and are thus similar to the Western Palaearctic Eumaeiti. The only representative of the Aphnaeini is obligatorily myrmecophilous as usual for this tribe, while the single members of the Miletinae, Curetinae and Lycaenini are all myrmecoxenous.

Overall, the majority of myrmecophilous lycaenids in Japan belongs to the tribe Polyommatini, whereas the lower proportion of myrmecophiles, when compared with the Western Palaearctic fauna, is due to the considerable diversity of one single largely myrmecoxenous subtribe, viz Thecliti.

Tab.11: Faunal composition and myrmecophily of Japanese Lycaenidae (given are species numbers). The first 3 columns refer to species with life-history information and direct evidence for ant-associations present. The latter 3 columns are based on the myrmecophily estimates for the entire fauna (see text). n: total species number, phil: myrmecophilous, obl: obligatorily myrmecophilous.

Taxon	Species with information available			Entire fauna		
	n	phil	obl	n	phil	obl
Poritiinae	-	-	-	-	-	-
Miletinae	1	0	0	1	0	0
Curetinae	1	0	0	1	0	0
Lycaeninae	59	25	5/6?	59	34	5/6?
Aphnaeini	1	1	1	1	1	1
Lycaenini	1	0	0	1	0	0
Theclini	25	4	1	25	4	1
Eumaeini	7	2	0	7	4	0
Polyommatini	25	18	3/4?	25	25	3/4?
Lycaenidae	61	25	5/6?	61	34	5/6?

One must be aware that, for zoogeographical considerations, Japan is only a depauperate appendix of the Eastern Palaearctic. The lycaenid fauna of continental East Asia is much more diverse and, in particular, contains a larger number of species of myrmecophilous taxa like Polyommatiti or (towards the south) Arhopaliti.

Unfortunately, no comprehensive and taxonomically modern faunistic study of Chinese and East Siberian lycaenids is available, and the ecology of East Asian Lycaenidae is largely unknown. Hence, a detailed analysis of the Eastern Palaearctic is yet impossible, but most likely the proportion of myrmecophiles will turn out to be higher than in Japan, approaching the level of the Western Palaearctic (60—80 %).

Australia

Australia houses a lycaenid fauna of 133 known species, all of which belong to the sub-family Lycaeninae except a single representative of the Miletinae-Liphyrini. The ecology of Australian lycaenids is rather well known, the main source of data being the book of Common & Waterhouse (1981). Further information was derived from Grund & Sibatani (1975), Storey & Lambkin (1983), Atkins & Heinrich (1987), Hawkeswood (1987), Valentine & Johnson (1988), Samson (1989), Lambkin & Samson (1989), Braby (1990), and others.

Published information was found for 109 species, 74 of which (67.9 %) are myrmecophilous, including 28 obligately ant-associated species (25.7 %). The estimates for the entire fauna (133 species) yield about 120 myrmecophiles (90.2 %), including about 45 obligate ones (33.8 %).

These estimates are based on the assumption that only very few of the Theclini and Polyommatini (e.g. some *Philiris* species and the genus *Neolucia*) and a couple of Eumaeini (genus *Deudorix*) will finally turn out to be truly myrmecoxenous. For all other genera or species groups represented in Australia, close relatives are known to be ant-associated, lending support to the assumption that these groups as a whole are myrmecophilous.

The high proportion of obligate associations is still a rough estimate, since for a number of species in the genera *Hypochrysops, Jalmenus*, and *Ogyris* the obligateness of ant-associations requires further investigation. In any case, the Australian lycaenid fauna has both, a very high proportion of myrmecophiles in general (70—90 %) as well as a high percentage of obligate relationships to ants.

These figures are fairly close to the results of Pierce (1987) who gave a proportion of 72 % myrmecophilous lycaenids, including 35 % obligately ant-associated species. Some minor differences are due to more recently published information. However, my systematic estimate for the whole Australian fauna yields an even more extreme prevalence of myrmecophily, suggesting that, with very few exception, almost all Australian lycaenids are at least weakly ant-associated.

Again there is a significant systematic pattern. The Australian lycaenid fauna comprises two equally large tribes (Theclini and Polyommatini), while Deudorigiti and Liphyrini together contribute only 9 species. Within the Theclini, the endemic subtribes Luciiti, Ogyriti and Zesiiti are almost entirely myrmecophilous, as are the few members of the Oriental Arhopaliti in northern Australia.

Within the Polyommatini, the endemic Candaliditi and the *Theclinesthes* section of the Polyommatiti contribute most to the species diversity and are myrmecophilous with very few exceptions. The Eumaeiti contain a small number of myrmecoxenous species, but all typically myrmecoxenous systematic groups (Poritiinae, Curetinae, Lycaenini, Thecliti) are absent from Australia.

Australia is just a part of the Austro-Melanesian zoogeographical region southeast of Wallace's line. However, the present knowledge of the systematics and ecology of the

Tab.12: Faunal composition and myrmecophily of Australian Lycaenidae (given are species numbers). The first 3 columns refer to species with life-history information and direct evidence for ant-associations present. The latter 3 columns are based on the myrmecophily estimates for the entire fauna (see text). n: total species number, phil: myrmecophilous, obl: obligatorily myrmecophilous.

Taxon	Species with information available			Entire fauna		
	n	phil	obl	n	phil	obl
Poritiinae	-	-	-	-	-	-
Miletinae	1	1	1	1	1	1
Curetinae	-	-	-	-	-	-
Lycaeninae	108	73	27	132	119	≈43
Aphnaeini	-	-	-	-	-	-
Lycaenini	-	-	-	-	-	-
Theclini	50	44	24	62	58	≈40
Eumaeini	8	2	1	8	3	1
Polyommatini	50	27	2	62	58	2
Lycaenidae	109	74	28	133	120	≈45

Lycaenidae of New Guinea and its surrounding islands is too scanty to allow a more comprehensive analysis. There is some indication that the overall level of myrmecophily is somewhat lower in New Guinea.

Typically myrmecoxenous groups missing in Australia (Curetinae, Lycaenini) are at least weakly represented there, and the rather large genus *Philiris* (>60 species) appears to have a low level of myrmecophily (Forbes 1977, Parsons 1984, Wood 1984). Thus, the proportion of myrmecophiles in the entire Austro-Melanesian region may probably amount to 75—85 %.

Thailand and West Malaysia

The Lycaenidae fauna of the Oriental region is very rich in species with peak diversity in South East Asia ("Sundaland"). From the island Borneo alone 375 Lycaenidae species, i.e. more than three times the species diversity of Europe, are known (Seki et al. 1991). Thailand and West Malaysia are sufficiently well surveyed from the faunistic point of view (Corbet & Pendlebury 1978, Pinratana 1981) to allow at least a preliminary analysis of the distribution of myrmecophily, although ecological data are available only for a limited number of species.

The main aim of the inclusion of this area in the zoogeographical considerations is to provide data for one of the most species-rich parts of the world. Pierce (1987) only discussed India as part of the Oriental fauna, but this subcontinent has far less lycaenid species and its fauna is, to the north, strongly mixed with Palaearctic elements (e.g. in the Himalaya).

In total, approximately 450 Lycaenidae species occur in Peninsular Malaysia and Thailand with ecological information found for 119 species. Seventy-one of those (59.7 %) are known to be ant-associated including 7—14 (5.9—11.8 %) obligate myrmecophiles (this uncertainty is caused by the lack of sufficient new data).

Viewing at the whole fauna, an estimated maximum of 370 species (82.2 %) are myrmecophilous with probably less than 80 (17.8 %) obligatory cases. This estimate is based on the following assumptions.

All Poritiinae, Curetinae and Lycaenini are myrmecoxenous (this is true for all well documented Oriental members). In contrast, all Aphnaeini are myrmecophilous and probably even obligatorily so. Within the Miletinae, about 20 species are suspected to have a more than casual relationship towards ants, using ants as oviposition cues (like *Allotinus unicolor, Miletus* spp.) or even as larval food (probably less than 10 species of obligate myrmecophiles like *Liphyra brassolis, Allotinus apries?*). These high estimates are surely upper limits.

For the Theclini I have assumed that all Arhopaliti are myrmecophilous (as is true for all sufficiently well documented species), whereas the few Thecliti are supposedly myrmecoxenous, as are most of their temperate zone counterparts. I suppose that less than 50 Arhopaliti will finally turn out to be obligately myrmecophilous, but given the poor knowledge of that group this is a rather arbitrary figure.

In the Eumaeiti reductions of myrmecophily may be fairly common (only about one half of the Oriental species, for whom information is available, is surely ant-associated), and the assumption of less than 110 myrmecophilous species is certainly a very high upper limit. Within the Polyommatini most species are assumed to be myrmecophilous, but the figure of 10 obligate ant-associations is again almost certainly an overestimation (only one species, *Anthene emolus*, is yet certainly documented as being an obligate myrmecophile).

Thus, the true values for the proportion of myrmecophiles in general, and for obligate myrmecophiles among the lycaenid fauna of West Malaysia and Thailand, may well be lower than the above estimates ($<$ 80 % and $<$ 15 %, respectively).

Since the systematic structure has been used to construct these estimates, an analysis of systematic effects on the distribution of myrmecophily must be restricted to those cases with appropriate information available. An inspection of the data shows that the typical patterns are corroborated: a high proportion of myrmecophiles in the Aphnaeini, Theclini, and Polyommatini, with Eumaeini distinctly behind. Poritiinae, Curetinae, and Lycaenini are in fact myrmecoxenous, whereas the Miletinae contain a few specialized myrmecophiles.

This suggests that in South East Asia the proportion of myrmecophiles among the Lycaenidae fauna is rather high due to the preponderance of largely myrmecophilous taxa, but does not reach the extreme figures of Australia. The proportion of obligatorily myrmecophilous species, as well, is almost certainly distinctly lower than in Australia (10—20 %).

India

At present, a modern treatment of the Indian Lycaenidae is not available. For the purpose of this analysis I have thus compiled a preliminary species list using various sources (e.g. Bell 1915, Sevastopulo 1973, Pinratana 1981, Larsen 1987). This yielded a

Tab.13: Faunal composition and myrmecophily of Thai and West Malaysian Lycaenidae (given are species numbers). The first 3 columns refer to species with life-history information and direct evidence for ant-associations present. The latter 3 columns are based on the myrmecophily estimates for the entire fauna (see text). n: total species number, phil: myrmecophilous, obl: obligatorily myrmecophilous.

Taxon	Species with information available			Entire fauna		
	n	phil	obl	n	phil	obl
Poritiinae	1	0	0	27	0	0
Miletinae	14	7	2/4?	35	20 ?	10?
Curetinae	4	0	0	10	0	0
Lycaeninae	100	64	5/10?	378	<350	<70
Aphnaeini	2	2	2	7	7	7
Lycaenini	2	0	0	6	0	0
Theclini	14	11	1/4	132	130	<50?
Eumaeini	40	19	1	130	<110?	1?
Polyommatini	42	32	1/3?	103	<100	10?
Lycaenidae	119	71	7/14?	450	<370	<80?

minimum number of 247 species occurring in India, but due to the weak representation of the Himalaya region this is certainly an underestimate, the actual diversity being probably in the range of 300 species.

For 114 Indian lycaenid species ecological information was found with about 90 (78.9 %) being ant-associated, including 11—12 obligate myrmecophiles (ca. 10 %). Using these data and considering the taxonomic affinities, about 175—195 of the 247 recognized species are probably myrmecophilous (71—79 %) with some more than 20 (8.1 %) obligate myrmecophiles.

These estimates are again based on the assumption that Poritiinae, Curetinae, Lycaenini and Thecliti are myrmecoxenous, Aphnaeini and Arhopaliti are entirely myrmecophilous, and Polyommatinae are mostly myrmecophilous with few exceptions. The Eumaeini are considered to be largely myrmecophilous as well, but with a considerable number of myrmecoxenous species in the Deudorigiti, as suggested by the available evidence.

A comparison with the data of Pierce (1987) indicates some minor differences:
— First, Pierce based her study solely on the work of Bell (1915) and thus considered only 60 species.
— Secondly, the overall proportion of myrmecophiles is given with 75 %, which is practically identical to my results.
— Thirdly, she stated that 22 % of the Indian lycaenids investigated by Bell (i.e. 13 spp.) were obligate myrmecophiles. My data give a very similar absolute number of obligate myrmecophiles, but yield a distinctly lower percentage. This is most likely explained by the fact that obligate ant-associations are rather conspicuous in the field and have most strongly attracted the attention of the early lepidopterists, while myrmecoxenous species or rather weak ant-associations are underrepresented in Bell's work.

Thus, the overall pattern is that in India about 70—80 % of the Lycaenidae are ant-associated, but obligatory myrmecophily probably occurs in only about 10 % of the species.

The systematic faunal structure well explains this pattern. All known Aphnaeini larvae, and most Theclini and Polyommatini caterpillars are myrmecophilous, while about one fourth of the Eumaeini and all Curetinae, Poritiinae, and Lycaenini are myrmecoxenous. The myrmecophilous higher taxa clearly dominate the Indian fauna, but the myrmecoxenous taxa are sufficiently well represented to reduce the proportion of myrmecophiles to roughly the same level as in Europe or South East Asia.

Tab.14: Faunal composition and myrmecophily of Indian Lycaenidae (given are species numbers). The first 3 columns refer to species with life-history information and direct evidence for ant-associations present. The latter 3 columns are based on the myrmecophily estimates for the entire fauna (see text). n: total species number, phil: myrmecophilous, obl: obligatorily myrmecophilous.

Taxon	Species with information available			Entire fauna		
	n	phil	obl	n	phil	obl
Poritiinae	-	-	-	1	0	0
Miletinae	4	2	1/2	5	2	1/2
Curetinae	2	0	0	4	0	0
Lycaeninae	109	88/89	10	237	180/190	>18
Aphnaeini	3	3	3	9	9	9
Lycaenini	6	0	0	11	0	0
Theclini	15	13	3?	57	42	>3
Eumaeini	35	27	1	71	>53	1?
Polyommatini	50	45/46	3?	89	>77	5?
Lycaenidae	115	90/91	11/12	247	185/195	>20

South Africa

The South African lycaenid fauna (delimitations of the area considered following Pennington et al. 1978) is rather well known from both, systematics and ecology. According to Pennington et al. (1978) and updated with some more recent systematic treatments (e.g. Henning 1979, Henning & Henning 1984, 1989, Migdoll 1988, Bridges 1988), the lycaenid fauna of South Africa comprises about 341 species.

Life-history information is present for 208 species (main sources besides the above cited papers: Cottrell 1965, Clark & Dickson 1971, van Someren 1974, Sevastopulo 1975, Claassens & Dickson 1980, Henning 1983a, b, 1984a, b), with 104—109 ant-associated ones (50—52.4 %) including at least 55 obligate myrmecophiles (26.4 %). An extrapolation to the whole South African lycaenid fauna yields about 270 myrmecophilous species (79.2 %) including roughly 180 obligate myrmecophiles (52.8 %).

The reasoning for the latter estimates is as follows. The rather few Poritiinae and Lycaenini are suspected to be entirely myrmecoxenous, whereas the Aphnaeini are supposedly all myrmeco-

philous. Within the Polyommatini, the vast majority is myrmecophilous as well, with only few secondary reductions in the *Uranothauma* section. The Eumaeini probably contain a higher proportion of secondarily myrmecoxenous species (in the genera *Deudorix* and *Capys*, and possibly in *Iolaus*).

The South African Miletinae are, in contrast to their Oriental relatives, probably largely myrmecophilous, but this is due to the preponderance of one single genus, *Thestor*, which is subdivided in a number of local endemics in southern Africa and apparently has a close association with the ant genus *Acantholepis* (Clark & Dickson 1971, Claassens & Dickson 1980).

The extraordinarily high estimate for the proportion of obligate myrmecophiles in South Africa requires further explanation. The large number of presumed obligate myrmecophiles is due to only three systematic groups. One is the Miletinae genus *Thestor* with about 24 South African species.

The second group is the Polyommatini genus *Lepidochrysops* with about 55 South African species. Nearly all *Lepidochrysops*, whose life-history is sufficiently well known, live as parasites in *Camponotus* nests during the third and fourth larval instar (Cottrell 1965, 1984, Clark & Dickson 1971, Claassens 1976, Henning 1983a, b). It is strongly suspected that most *Lepidochrysops* species have a similar life-cycle.

The most diverse group of obligate myrmecophiles are the Aphnaeini with 124 recognized species in South Africa, and there is strong evidence that more than 70 % of this tribe are obligatorily associated with ants, mostly from the genus *Crematogaster*. Together, this results in the high estimate of more than 50 % of the South African lycaenids being obligatorily ant-associated. Henning (1987b) arrived at the same estimate.

A comparison with the figures of Pierce (1987) demonstrates significant differences. Pierce's evaluation was largely based on the works of Clark & Dickson (1971) and Claassens & Dickson (1980). The former exclusively covers species bred by the authors, while the latter is only concerned with a small subregion, the Table Mountain range.

Hence, Pierce (1987) considered only 107 species, 99 of which are myrmecophilous with a proportion of 27 % obligate myrmecophiles. This restricted range of species considered is the major reason for the differences between Pierce's analysis and the above one. The myrmecoxenous Poritiinae are distinctly under-represented in the books of Clark & Dickson (1971) and Claassens & Dickson (1980) and, accordingly, the overall proportion of myrmecophiles in the analysis of Pierce is probably too high.

In contrast, the species-rich genera *Thestor* (Miletinae), *Aloeides, Poecilmitis* (Aphnaeini), and *Lepidochrysops* (Polyommatini) are only partially treated in the above mentioned works, resulting in too a low estimate of the proportion of obligate myrmecophiles in the paper of Pierce (1987).

As has already pointed out above, the systematic faunal composition contributes importantly to the proportion of facultative and obligate myrmecophiles among the South African Lycaenidae. Two highly myrmecophilous taxa, Aphnaeini and Polyommatini, alone account for 70 % of the whole species diversity, supplemented by myrmecophilous members in the Miletinae and Eumaeini. The myrmecoxenous taxa Poritiinae and Lycaenini, in contrast, constitute less than 10 % of the lycaenid fauna.

In this respect, however, South Africa is not representative for the whole Ethiopian region. In tropical Africa, in particular, the Poritiinae-Liptenini form a significant compound (35 %) of the fauna. Supposing that at least half of them are truly myrmeco-

Tab.15: Faunal composition and myrmecophily of South African Lycaenidae (given are species numbers). The first 3 columns refer to species with life-history information and direct evidence for ant-associations present. The latter 3 columns are based on the myrmecophily estimates for the entire fauna (see text). n: total species number, phil: myrmecophilous, obl: obligatorily myrmecophilous.

Taxon	Species with information available			Entire fauna		
	n	phil	obl	n	phil	obl
Poritiinae	14	0	0	30	0	0
Miletinae	12	4/9?	3/8?	27	≈ 24?	≈ 24?
Curetinae	-	-	-	-	-	-
Lycaeninae	182	100	>50	284	>245	>155
Aphnaeini	61	45	>35	124	124	>100
Lycaenini	2	0	0	2	0	0
Theclini	-	-	-	-	-	-
Eumaeini	35	9	0	43	>20	0
Polyommatini	84	46	>16	115	≈102	56
Lycaenidae	208	104/109?	>55	341	≈270	>180

xenous, and further considering that secondary myrmecoxeny does occur in a number of African Deudorigiti (e.g. *Capys*), Polyommatiti (*Uranothauma* section), and possibly Iolaiti, this reduces the overall proportion of myrmecophiles in the entire Ethiopian region to well below 80 %.

Likewise, the percentage of obligate myrmecophiles decreases. If, as a rough approximation, all *Thestor* and *Lepidochrysops* species, 80 % of the Aphnaeini, and 20 % of the Lycaenesthiti (*Anthene* and related genera) are considered to be obligatorily associated with ants, this results in an absolute number of approximately 400 species (less than 30 % of the roughly 1500 Ethiopian lycaenids). For a more detailed and comprehensive analysis, more data from the tropical areas of Africa are clearly needed.

Neotropical region

The Neotropical lycaenid fauna is very rich in species (>1000), but only two higher taxa are represented: Eumaeiti (the vast majority) and Polyommatiti (far less than 50 spp.). Ecological data are very scant, and the taxonomy and faunistics are still in a premature state. Mainly from these reasons Pierce (1987) decided not to include the Neotropics into her analysis. I here give a very preliminary view which, nevertheless, should allow to estimate upper and lower limits for the proportion of myrmecophiles among the Neotropical lycaenids.

Life-history information is available for roughly 160 species occurring south of the United States (Tab.17 and Robbins, pers. comm.). More than 150 of the species covered belong to the Eumaeiti. The few Neotropical Polyommatini are poorly documented,

but several species of *Hemiargus*, *Brephidium* and *Zizula* are known to be myrmecophilous. The ecology of the Andine representatives of the *Hemiargus* group (Nabokov 1945) is unknown.

Ant-associations have been recorded for only 17 Neotropical Eumaeiti species (12.2 %), and no single case of myrmecophily among Neotropical Lycaenidae has yet surely been established as being obligatory. In contrast, 27 species (17.3 %) have been explicitly stated to have no ant-associations.

Assuming that closely related species (belonging to the same genus) have similar degrees of myrmecophily, the presumed percentage of myrmecophilous species increases to 27.6 %, while the proportion of myrmecoxenous Eumaeiti becomes 26.3 %. Notwithstanding the meagre database, the following conclusions can be drawn:

— First, myrmecophily is clearly less widespread and less strongly developed among the Eumaeiti than in other large lycaenid subtribes. Otherwise more ant-associations would have been reported, as it is the case for the tropical regions of Africa and Asia. The limited number of well documented myrmecophiles among the temperate zone Eumaeiti further corroborates this conclusion.

— Secondly, obligate myrmecophily is rare within the Eumaeiti, if it does occur at all. Obligate associations are more likely to be detected than facultative ones, especially in such species where larvae or pupae regularly occur inside ant nests. No such case is hitherto known from Neotropical lycaenids (but from Riodinidae: Harvey 1987, Ballmer, pers. comm.).

— Thirdly, reductions of myrmecophily have occurred several times in parallel. Examples are the genera *Eumaeus, Arcas, Contrafacia*, and *Erora*, where even the DNO is virtually absent.

Overall, the Neotropical lycaenid fauna appears to be characterized by a rather low proportion of myrmecophiles. Furthermore, many species presumably have only loose, facultative ant-associations, and obligate myrmecophily is surprisingly rare.

Nearctic region

North America's lycaenid fauna is taxonomically well known. Nevertheless, our knowledge of its ecology and larval myrmecophily is still incomplete. The majority of recorded ant-associations dates from the last decade (e.g. Harvey & Webb 1980, Ballmer & Pratt 1988, and in press, Harvey & Longino 1989). Therefore, further additions may well occur, in particular from species with arboricolous larvae where the available life-history information is largely based on oviposition records and subsequent laboratory rearings.

For 111 of the 112 resident lycaenid species of North America (species concepts following Scott 1986 and Ballmer & Pratt 1988, Riodinidae excluded) life-history information is available. Only 33 species (29.7 %) have been reported being ant-associated, 23 of those belonging to the Polyommatini, whereas only six Eumaeiti and four Lycaenini species are surely known to be myrmecophilous.

No Nearctic lycaenid is yet known to be obligatorily myrmecophilous, but since recent work on Swiss populations of the Holarctic Polyommatine *Plebejus idas* indicates that this species may have an obligate relationship to certain *Formica* ants (Jutzeler 1989d), it is well possible that North American populations do so as well.

An estimate for the whole Nearctic fauna yields at least 45 myrmecophilous species (40.2 %). It is very likely that all Polyommatini species, except the myrmecoxenous arctic or alpine genera *Agriades* and *Vacciniina*, are at least facultatively associated with ants. In addition, at least another four Eumaeiti species are supposed to be myrmecophilous, judging from their close relatives, but in the course of a more thorough knowledge of the ecology of Eumaeiti larvae in the field, this number may well increase further.

When comparing these figures with the data given by Pierce (1987), one has first to consider that in this latter paper the riodinids were treated as a lycaenid subfamily. Removing them, the 23 cases of ant-associations cited by Pierce give a 20.5 % proportion of myrmecophiles (total of 112 species). The differences to the analysis presented above are mainly due to the recent additions to the list of North American myrmecophiles by Ballmer & Pratt (1988, and in press) and Harvey & Longino (1989). When the systematic relatedness is taken into acount, this well doubles the percentage given by Pierce (1987).

As in all other zoogeographical regions considered here, the systematic structure of the Nearctic lycaenid fauna closely parallels the distribution of myrmecophily. Ant-associations are unknown from the Miletinae and Thecliti (only 3 species altogether), but are abundant among the Polyommatini. Only 10 % of the Nearctic resident Eumaeiti have hitherto been reported being myrmecophilous, and 4 of 15 Lycaenini species have evolved an interesting alternative pathway towards myrmecophily.

The predominance of one subtribe with a pronounced tendency to reduce ant-associations (the Eumaeiti contribute 53.6 % to the species diversity) is responsible for the rather low overall proportion of myrmecophiles among the North American Lycaenidae.

Tab.16: Faunal composition and myrmecophily of North American Lycaenidae (given are species numbers). The first 3 columns refer to species with life-history information and direct evidence for ant-associations present. The latter 3 columns are based on the myrmecophily estimates for the entire fauna (see text). n: total species number, phil: myrmecophilous, obl: obligatorily myrmecophilous.

Taxon	Species with information available			Entire fauna		
	n	phil	obl	n	phil	obl
Poritiinae	-	-	-	-	-	-
Miletinae	1	0	0	1	0	0
Curetinae	-	-	-	-	-	-
Lycaeninae	110	33	1?	111	≈45	1?
Aphnaeini	-	-	-	-	-	-
Lycaenini	15	4	0	15	4	0
Theclini	2	0	0	2	7	0
Eumaeini	60	6	0	60	≈10	0
Polyommatini	33	23	1?	34	31	1?
Lycaenidae	111	33	1?	112	≈45	1?

Conclusions

1.) In contrast to the opinion of Pierce (1987), most higher taxa of the Lycaenidae show peculiar and characteristic distributions. These distributions correspond well to the continental plates, or subregions of those: Liptenini, Liphyrini, Aphnaeini and Lycaenesthiti are centred in Africa; Luciiti, Zesiiti, and Candaliditi in Austro-Melanesia; Poritiini, Miletini, Curetinae, Arhopaliti, Catapaecilmatiti, Loxuriti, Remelaniti, and Niphanditi in southern Asia; Thecliti in East Asia; and Eumaeiti in the Neotropics.

Most of these tribes or subtribes are even restricted to the above mentioned regions, while others weakly extend into adjacent realms. As a consequence, these distributional patterns result in characteristic and very different systematic compositions of the lycaenid faunas of all regions investigated.

Although the detailed phylogenetic relationships between the higher lycaenid taxa are not yet clear, the observed patterns strongly point towards historical and evolutionary processes associated with plate tectonics. Obviously, the evolution of the higher lycaenid taxa is strongly correlated with the break-up of the Mesozoic south continent Gondwana. This connection of the Lycaenidae to Gondwana was already noted by Pierce (1987).

The north continent Laurasia probably had no lycaenid fauna when it separated from Gondwana, and since North America split off early from the remainder of the north continent ("proto-Eurasia"), it became isolated for a long period and was only late colonized by lycaenid stocks from South America (Eumaeiti) or Asia (Polyommatiti). Only the Nearctic Miletinae *Feniseca tarquinius* may have entered North America from Europe via the Thule bridge during the Tertiary.

The eastern part of the north continent ("proto-Eurasia"), as well, seems to have been only secondarily colonized by lineages from the south (via the Iberian bridge in the southwest and via Sundaland in the southeast: Eliot, pers. comm.), indicating that the primary evolution of higher lycaenid taxa took place in Gondwana and its subsequent fragments.

The details of this story remain to be uncovered. In particular, the role of India and Australia are a matter of debate: Do the Australian endemics (Luciiti, Ogyriti, Candaliditi) represent an ancient stock, or did they colonize Australia secondarily? Did India carry any significant lycaenid fauna from Africa towards Asia?

In any case, one major event in the break-up sequence of Gondwana, the separation of South America from Africa, has a close parallel in the distribution of lycaenids: the African and Oriental Deudorigiti and their Neotropical sister-group Eumaeiti.

2.) The characteristic distributional patterns of higher lycaenid taxa, and the resulting different faunal structures due to the subsequent radiation of these taxa, have a significant corollary with respect to myrmecophily. Regions where taxa with a low level of myrmecophily predominate (Thecliti in eastern Asia, Eumaeiti in the Americas), must necessarily have a lower proportion of myrmecophiles than regions with a preponderance of highly myrmecophilous groups (e.g. Aphnaeini and Polyommatini in Africa, Polyommatini in Europe, Polyommatini and Theclini in Australia).

Thus, again contradicting the work of Pierce (1987), the evolutionary histories and faunal compositions of the different zoogeographic regions do explain, to a considerable degree, the observed geographical patterns of myrmecophily.

3.) The clear-cut north-south disparity in the proportion of myrmecophily claimed by Pierce (1987) could not be confirmed. Instead, in most areas of the Old World, including the Western Palaearctic (Fiedler 1991), the proportion of myrmecophiles is 70—80 %. A higher value may occur in Australia with its depauperate and specialized fauna, and lower percentages occur in Japan (a depauperate part of the Eastern Palaearctic) and in the New World. All these deviations are easily explained by the respective faunal compositions, i.e. by their colonization history. Two examples may illustrate this.

North America, with its low proportion of myrmecophiles, was mainly colonized by three lineages. The myrmecoxenous Lycaenini and the myrmecophilous Polyommatini arrived from the Palaearctic through a northern route. Climatic constraints possibly limited a more extensive invasion, but both taxa largely retained their characteristic relationships to ants. A few Polyommatini (*Leptotes, Zizula, Brephidium*) are supposed to have arrived via wind dispersal across the Atlantic ocean, and these as well have retained the myrmecophily of their African relatives.

The Eumaeiti invaded from the Neotropics without changing much their already low level of myrmecophily. This southern route allowed a more extensive invasion, resulting in the preponderance of Eumaeiti in the today North American lycaenid fauna.

Thus, there is no reason to assume that ecological (abiotic or biotic) factors primarily caused the rather low proportion of myrmecophily in the Nearctic, although the climate may well have secondarily shaped the level of ant-associations (reductions of myrmecophily appear to be favoured in arctic or alpine tundra habitats, in boreal forests, or in the canopy of temperate zone Fagaceae forests; see above).

The Western Palaearctic, with its high proportion of myrmecophiles, has a completely different history. Although the majority of the lycaenid fauna was certainly exterminated during the glaciations, refugial areas existed in the Mediterranean area and in non-glaciated regions of Asia. As a consequence, a rapid recolonization was possible, allowing a rather rich fauna of largely myrmecophilous Polyommatini to invade into Europe again.

Other tribes only survived or recolonized in limited numbers, whereas the tropical subfamilies Poritiinae, Miletinae, and Curetinae did not manage to cross the geographical barriers (North African and Arabian deserts, Western and South Central Asian mountain ranges). Again climatic factors have secondarily shaped the level of myrmecophily, e.g in high latitudes.

4.) The north-south disparity in the obligateness of myrmecophilous associations remains to be further investigated. In the Palaearctic, only about 10 % of the lycaenids are obligatorily myrmecophilous. A similar estimate was attained for India. In South East Asia, the obligate myrmecophiles most likely constitute less than 20 % (and possibly less than 15 %) of the entire lycaenid fauna.

In contrast, South Africa (27 %) and Australia (35 %) have very high percentages of obligate myrmecophiles, whereas among the New World lycaenid fauna, although less well understood, such associations appear to play almost no role.

These data indicate that, instead of a clear-cut disparity, a gradient in the proportion of obligatory ant-associations is likely to exist. The highest percentages occur in South Africa and Australia, the lowest in the Palaearctic, with the more tropical regions of India, South East Asia, or New Guinea apparently being intermediate.

Whatever the exact figures may be, distinct differences in the obligateness of ant-associations between several zoogeographical regions seem to be real. The question as to what evolutionary processes have led to this pattern will be discussed, among others, in the final chapter.

EVOLUTION OF INTERACTIONS BETWEEN LYCAENIDS AND ANTS

Ants as selective agents for lepidopterous caterpillars

The leading role of ants as predators of arthropods (e.g. Hölldobler & Wilson 1990) has often been demonstrated. Rather slowly moving and weakly sclerotized organisms like most Lepidoptera caterpillars, in particular, provide nearly prototypical ant prey.

As a consequence, predatory ants are important regulators of caterpillar abundance (e.g. the ant genus *Formica*: Laine & Niemelä 1980, Gösswald 1989) that significantly influence the overall level of herbivory (Warrington & Whittaker 1985) or may even shape the guild structure of phytophagous caterpillars (Ito & Higashi 1991).

The influence of ants on caterpillar survival may differ between larval instars or between various ant species (Tilman 1978, Weseloh 1989), and it may further interfere with the caterpillars' parasitism rate (Jones 1987). Clearly, ant predation is a weighty selective pressure for Lepidoptera larvae, and a number of life-history traits and adaptations of the latter may be seen, at least in part, as a defensive response towards ants.

Bernays & Cornelius (1989) observed that the ant *Iridomyrmex humilis* preferentially preyed upon polyphagous caterpillars, suggesting that food specialists (especially monophagous species) are typically more effective in the extraction and storage of toxic plant chemicals which help to deter predators (see also Bernays 1988).

Further support for this hypothesis comes from the studies of Bernays & Montllor (1989) and Bowers & Larin (1989) who observed that aposematic caterpillars feeding on toxic plants (*Uresiphita reversalis* [Pyralidae] and *Eumaeus atala* [Lycaenidae]) were rejected by ants as prey. However, the aposematic caterpillars of the arctiid moth *Tyria jacobaeae*, although sequestering considerable amounts of pyrrolizidine alkaloids, are heavily preyed upon by ants (Myers & Campbell 1976, Vrieling et al. 1991).

Generally, the use of plant semiochemicals is extremely widely distributed among the Lepidoptera as defensive device (for a review see Brower 1984), and it should be noted that the majority of Lycaenidae caterpillars are food specialists (see above) whose hostplants contain toxic secondary compounds (cyanogenic glycosides, alkaloids, and others).

A more elaborated way of chemical defence, when disturbed, is the regurgitation of foregut contents with toxic plant semiochemicals (Common & Bellas 1977, Eisner et al. 1980, Brower 1984, Leather & Brotherton 1987, Peterson et al. 1987), or the release of defensive secretions from specialized exocrine glands (e.g. Eisner et al. 1970, 1972, Honda 1983a, b, Witthohn & Naumann 1987).

In the examples mentioned here these defensive devices have been shown to be effective against ants. Numerous lycaenid larvae also regurgitate when disturbed (e.g. *Polyommatus coridon*: Fiedler, unpublished), and since the latter species feeds on cyanogenic hostplants (*Hippocrepis, Coronilla*) its regurgitations may provide a powerful defense.

Numerous other protective adaptations have evolved among the Lepidoptera. Many caterpillars are hairy (e.g. Lasiocampidae, Arctiidae, Lymantriidae), and this provides

some protection against ant attacks at least in later larval instars (Ayre & Hitchon 1968, Tilman 1978). Other caterpillars escape by dislodging on silk threads (e.g. Leather & Brotherton 1987), but this strategy is not invariably effective against ants (Allen et al. 1970). Further defensive behavioural responses to predatory attacks are dropping off from the hostplant, thrashing against potential enemies and others (Cornell et al. 1987), and all these may be involved in the defence against ants.

A very important protective life-history trait is endophytism. Endophytic larvae (those boring in stems or living in shelters of leaves spun together) are readily attacked and killed when deprived of their protective envelope (Bernays & Cornelius 1989), but in the field such larvae easily survive even in habitats densely populated with ants (Allen et al. 1970, Ito & Higashi 1991). Notably, numerous lycaenid caterpillars (especially in the Deudorigiti and Eumaeiti, see above) are endophytic.

These examples may suffice to demonstrate that ant predation is an important selective agent in the evolution of Lepidoptera caterpillars and that a number of defensive or protective mechanisms are realized within this large taxon of herbivorous insects.

Nevertheless, the ants must be viewed differentially as well. Whereas some ant sub-families are entirely or predominantly predatory (Ponerinae, Ecitoninae, Dorylinae), others contain a large proportion of trophobiotic species (Pseudomyrmecinae, Myrmicinae, Dolichoderinae, Formicinae). Indeed, the trophobiotic ant subfamilies contribute most to the species diversity of the family Formicidae.

Furthermore, the level of ant predation shows a marked latitudinal gradient (Jeanne 1979) with the highest predatory pressure arising from ants in the tropics.

Thus, the complex of adaptations that allows caterpillars to avoid the attacks of trophobiotic ants — and only these are involved in myrmecophily of butterfly caterpillars (DeVries 1991, this study) — yields an enormous twofold selective advantage. A large number of ant species is excluded from the potential enemy guild, and this coexistence with ants enables these caterpillars to colonize ecological niches with a high abundance of ants, but distinctly fewer competitors and enemies ("enemy-free space": Atsatt 1981a).

As has already been emphasized by Lenz (1917) and Malicky (1969b, 1970a), this was certainly the leading selective advantage at the beginning of the evolution of lycaenid myrmecophily (see also DeVries 1991).

Evolution of myrmecophily and its related organs

As has been discussed in the systematic chapter in detail, myrmecophily must be viewed as an apomorphic strategy within the Papilionoidea, where it is confined to, and has independently evolved in, distinct groups of the families Riodinidae and Lycaenidae. In both families myrmecophily is highly correlated with the presence of specialized secretory ant-organs (Cottrell 1984, DeVries 1988, 1991, this study), and the extant primarily myrmecoxenous subfamilies lack such organs (Hamearinae in the Riodinidae; Poritiinae and Miletinae in the Lycaenidae: Harvey 1987, this study). Thus,

the caterpillars of these groups may serve as models for the ancestors of the myrmecophilous taxa. In this chapter I will discuss some ideas on the phylogeny of the Lycaenidae in connection with the evolution of their ant-organs and ant-associations.

Within the Riodinidae, the classification of Harvey (1987) suggests a convincing parallelism between the evolution of ant-organs and myrmecophily. The caterpillars of primitive subfamilies (Hamearinae, Euselasiinae) and of several Riodininae tribes (Riodinini, Symmachiini, Stalachitini etc.) are hairy, lack ant-organs, and are never associated with ants.

In the less advanced myrmecophilous tribe Eurybiini (and possibly in Mesosemiini, but available records need confirmation), a pair of tentacle nectary organs evolved, whose function is analogous to the DNO of lycaenid caterpillars. Eurybiini (with only 23 recognized species) have facultative and unspecific ant-associations.

In the two most advanced tribes, the sister-groups Lemoniini (about 70 species) and Nymphidiini (190 species), two further types of ant-organs are present: the anterior tentacle organs (with a function apparently analogous to the TOs of lycaenid larvae, i.e. activating and alerting attendant ants), and a pair of vibratory papillae that produce vibrational signals to communicate with ants (Cottrell 1984, DeVries 1988, 1990a).

Some Nymphidiini larvae bear a fourth type of organs possibly related to myrmecophily ("bladder setae"), and these species apparently maintain obligatory relationships to ants (*Azteca, Crematogaster*: Harvey 1987, DeVries, pers. comm.).

Thus, there is a parallel increase in the number of ant-organs present, complexity and prevalence of ant-associations, and species diversity from Eurybiini towards Lemoniini and Nymphidiini. In short, the evolution of riodinid myrmecophily can be summarized by the sequence: protective devices (hairiness: coexistence) — trophobiotic glands (tentacle nectary organs: loose facultative mutualism) — communicative organs (anterior tentacle organs, vibratory papillae: stable mutualisms) — specific secretory organs ("bladder setae": obligate mutualisms).

The evolutionary sequence within the Lycaenidae is less clear. Since the hypothesis of ancestral myrmecophily (Pierce 1987, Scott & Wright 1990) had to be rejected by evidence from a systematic comparison (this study), myrmecophilous organs are supposed to have been absent in the caterpillars of ancestral Lycaenidae. A reasonable assumption is that ancestral lycaenid caterpillars resembled the larvae of extant Poritiinae or, possibly, Hamearinae.

If this is true, then the ancestral lycaenid larvae can tentatively be reconstructed as rather small, slowly moving, moderately hairy insects, which most likely already possessed lenticle-like setae. Modern Poritiinae effectively coexist with ants based on these "passive" preadaptations. It is yet unknown whether or not the typical leathery cuticle of higher lycaenids belonged to the groundplan of lycaenid caterpillars, as well.

The ability to completely retract the head under the prothoracic shield is well developed only in some Miletinae and the Lycaeninae tribes Lycaenini, Theclini, Eumaeini and Polyommatini, whereas Curetinae and Aphnaeini larvae lack this character. Therefore, this significant adaptation is very likely not a groundplan character of the Lycaenidae,

but has convergently evolved in two taxa whose larvae regularly interact with ants (homopterophagous Miletinae, myrmecophilous Lycaeninae).

Two plant taxa are candidates for being the primary lycaenid hostplants: Fabales (as modern Curetinae) or, perhaps less likely, Fagales (as *Poritia erycinoides*).

Probably, the larvae of ancestral lycaenids were primarily not truly attractive to ants. From behavioural observations there is no indication that the lenticles or pore cupola organs of Poritiinae, Miletinae, Curetinae, or Riodinidae produce secretions attractive to ants (see above). The tight connection of the PCOs to myrmecophily seems to be an apomorphic, secondary trait of the subfamily Lycaeninae, and these organs probably changed their function at least once during lycaenid phylogeny. It cannot be ruled out, however, that the ancestral PCOs could have played a role in mediating "ignorance" or "appeasement", but the chemical basis of these preadaptations for myrmecophily is not yet understood (DeVries 1991).

At any rate, the hypothetical ancestral lycaenid caterpillars were able to colonize habitats abundantly populated with ants. Such microhabitats are plants bearing extrafloral nectaries, plants colonized with trophobiotic Homoptera, or plants supporting ant nests. This is evidently a considerable selective advantage, since "normal" herbivorous caterpillars require special and often rather costly defensive adaptations to survive in such habitats. Three major lycaenid lineages have radiated starting from this primary myrmecoxeny.

The Poritiinae are the most diverse group of these. One of their tribes, the Oriental Poritiini, remained phytophagous, but nothing is known on their interactions with ants. The African tribe Liptenini tremendously diversified (today 520 species) in a very unusual nutritional niche: they specialized upon lichens. Liptenini larvae are known to coexist with ants where the latter are very abundant, and some species are presumed to maintain even commensalic relationships to the ant genus *Crematogaster*.

Since feeding on lichens and on detritus require similar specializations of ingestion and metabolism (Rawlins 1984), lichenivorous insects are possible candidates for the evolution of scavenging or refuse-feeding life-habits in ant nests (see also Ayre 1958).

Thus, Poritiinae larvae demonstrate the evolutionary effectiveness of coexistence with ants, but their greatest diversity probably evolved in relation to an unusual host shift. Overall, Poritiinae larvae never evolved specialized ant-organs and their interactions with ants are mostly governed by protective adaptations.

The subfamily Miletinae made a significant shift in larval nutrition towards aphytophagy. Atsatt (1981a) and Cottrell (1984) have discussed possible pathways leading to these highly untypical feeding habits. They assume that Miletinae carnivory started from ancestors feeding on fruits and other protein-rich plant parts. Given the presumed sister-group relation between Poritiinae and Miletinae, however, the ability to metabolize chitinous fungal components of lichens could as well represent a phyletic predisposition for carnivory. Only a better resolved phylogeny can help to decide between these alternatives.

Irrespective of this, Miletinae caterpillars as predators of Homoptera were regularly confronted with aggressive ants that defend their honeydew sources. Accordingly, Miletinae larvae were only able to exploit this food resource on the grounds of protective adaptations against ant-attacks. In fact, ants usually ignore highly adapted Miletinae caterpillars (*Miletus, Allotinus, Logania, Megalopalpus, Aslauga*), while less advanced genera (*Feniseca, Taraka, Spalgis*) additionally construct protective silken shelters wherein the larvae live, or they cover themselves with remains of their prey.

There is no evidence that Miletinae larvae in general secrete substances attractive to ants, their PCOs eliciting little interest in the ants attending homopterans. Some specialized taxa, however, became true myrmecophiles, pupating in ant nests (*Miletus*: the pupae posess glands highly attractive to ants; Roepke 1919), feeding inside ant nests on grubs (*Liphyra, Thestor?, Allotinus apries?*), or even eliciting trophallactic regurgitations (*Euliphyra*). These latter myrmecophiles are attractive to their host ants, possibly imitating their specific brood odour. Only *Liphyra* is regularly attacked, but resists ant-attacks due to its protective carapax-like cuticle (Cottrell 1987).

In all, the Miletinae represent a rather small taxon with amazing specializations, but its evolution is mainly based upon coexistence with ants, true myrmecophily having arisen several times independently from the carnivorous life-habits and the close association with trophobiotic ant-tended homopterans.

The third subfamily representing primary myrmecoxeny are the Curetinae. Their larvae feed on young foliage of Fabales where usually ants forage at extrafloral nectaries (DeVries 1984, Maschwitz & Fiedler, unpublished). Ants do neither attack the caterpillars, nor do they form close, stable associations with the latter. The peculiar TOs of *Curetis* larvae are defensive organs and are everted upon disturbance. No relation of the TOs or of the further specialized epidermal organs (DeVries et al. 1986) to myrmecophily is yet apparent.

In summary, larvae of the lycaenid subfamilies Poritiinae, Miletinae and Curetinae occupy ecological niches where the avoidance of ant-attacks is advantageous (plants with extrafloral nectaries) or even necessary (trophobiotic associations). Furthermore, their larvae possess a number of specialized epidermal organs, including TOs in two small subgroups, but none of these are hitherto known to be involved in interactions with ants.

The diversity of these three subfamilies is rather poor, representing less than 17 % of the described lycaenid species worldwide. Only one lineage (Liptenini) has diversified considerably in a distinct adaptive zone, viz. the shift towards lichenophagy.

With few secondary exceptions, the larvae of the primarily myrmecoxenous subfamilies were unable to achieve benefits beyond the enemy-free space from their "associations" with ants. Only Lipteniti caterpillars on trees infested with *Crematogaster* ants, or Miletinae larvae in trophobiotic associations or ant nests, probably enjoy some reduction of the pressure exerted by parasitoids or predators. Thorough ecological or behavioural investigations on these taxa are needed.

The most advanced subfamily Lycaeninae has transcended this spectrum of relationships with ants and has entered into mutualistic trophobiotic associations with ants. Unfortunately, the detailed historical sequence of the adaptive steps that have led to this true myrmecophily cannot yet be unravelled.

At the very beginning, myrmecoxenous larvae may have responded to ant-attacks with the exudation of small amounts of hemolymph or the production of frass pellets (compare the forced defaecation of aphids [*"Angstkoten"*] when attacked; or the anal exudates of the tortricid genus *Semutophila*: Maschwitz et al. 1986). Fresh moist caterpillar frass can be attractive to ants as it contains amino acids and possibly other nutritive plant compounds. I have repeatedly observed that lycaenid larvae (including myrmecophilous species) respond to occasional ant-attacks with defaecation (this study).

Certainly, the integration of the PCOs into the functional complex of ant-associations was an important early step in the evolution of Lycaeninae myrmecophily. PCOs and some further glandular setae suffice to induce stable ant-associations in some North American *Lycaena* species (Ballmer & Pratt 1988), and such associations possibly yield protective benefits to the caterpillars, although the ants receive only marginal rewards.

However, ant-associations of most *Lycaena* caterpillars and of other species without a functional DNO are fairly unstable even in the laboratory (this study), and they rarely occur in the field. Thus, the evolution of the DNO and its related nutritive secretions, as a keystone synapomorphy of the Lycaeninae, was obviously the decisive step towards myrmecophily. DNO secretions considerably improve the stability of ant-associations.

The histological investigations of Malicky (1969b) suggest that the DNO might have originated from glandular hairs, while Kitching & Luke (1985) imply that the DNO might be derived from secretory epidermal pores. A phylogenetic connection between the DNO and the abdominal glands of lymantriid caterpillars (Shields 1989b) lacks any supporting evidence and was already refuted by Malicky (1969b).

The evolutionary history of the TOs is less clear. The potential to evolve eversible structures must have been widespread in the Riodinidae and Lycaenidae. Two types of TOs in the Riodinidae are closely connected with myrmecophily, but among the Lycaenidae a relation of the TOs to ant-association is only known from the Aphnaeini and the higher Lycaeninae tribes, whereas the respective eversible organs of Curetinae and *Aslauga* (Miletinae) probably evolved independently in a different functional context (defence?).

The evolution of ant-related TOs in the Lycaeninae possibly started with glandular scent hairs. One can speculate that the volatile secretions of such hairs could be used more efficiently and economically, if the hairs are only extruded when required. Accordingly, cuticular sheaths and a mechanism for eversion and retraction were developed, leading to the complex TOs of extant lycaenids.

Malicky (1969b) suggested that DNO and TOs first evolved as metameric organs, that were later reduced on most body segments and were retained only in special locations. This hypothesis was mainly founded on the different locations of TO-like structures in

Riodinidae and Lycaenidae caterpillars, and on the presence of additional secretory structures ("dish organs") on some abdominal segments of certain Aphnaeini larvae.

However, since recent systematic and morphological work strongly indicates that myrmecophily and its related organs evolved independently in both families (e.g. DeVries 1990b, this study), the assumption of a multisegmental groundplan of ant-organs has to be rejected.

Given the very sporadic occurrence even among the Aphnaeini, the "dish organs" of *Spindasis* or *Crudaria* are peculiar apomorphic structures of these genera rather than being rudiments of ancestral nectary organs on additional abdominal segments. The apparent restriction of eversible glandular structures like the DNO and TOs to the fore or rear end of riodinid and lycaenid larvae may be due to interferences of the function of such organs with caterpillar locomotion.

Once the myrmecophilous organs had been developed, the enhancement of ant-associations via additional nutritive rewards (DNO) and communicative signals (TOs, vibrational communication?) must have resulted in a significant positive feed-back (higher rate of larval survival), and evidently this process reinforced the rapid evolution and radiation of larvae with a complete set of myrmecophilous organs.

The Aphnaeini, as the presumed first group that has split off from the Lycaeninae stem (Eliot 1973, and pers. comm.), even possess the most complex ant-organs (highly specialized TOs, "dish organs"). In this respect, the Aphnaeini might be viewed as an early "experimental" stage of lycaenid evolution, whereas later on the equipment with ant-organs, their morphology and function remained surprisingly constant. In fact, except the numerous reductions of myrmecophilous organs (see below) and the great diversity of secondary setae, the roughly 3300 species of the tribes Theclini, Eumaeini, and Polyommatini present a nearly monotonous view with regard to their ant-organs.

In short, the evolution of lycaenid myrmecophily may be simplified as follows:

1) only "passive" protective characters present (small, onisciform, moderately hairy, slowly moving caterpillars, PCOs present): coexistence with ants;

2) ant-attractive secretory organs evolve (PCOs become integrated into myrmecophily, trophobiotic DNO evolves): mutualism;

3) specific communicative signals evolve (chemical specialization of PCO and DNO secretions, pheromone mimics?): obligate mutualism or parasitism; or

4) trophobiotic glands become reduced: secondary myrmecoxeny.

In this scenario, a few myrmecophiles (Liptenini, Miletinae) have independently evolved from stage 1. The "typical" myrmecophily of lycaenid larvae is represented by stage 2, with alternatives 3 and 4 being optional. TOs may have evolved at stage 1 having later been integrated into communication with ants, or they could have evolved independently at stage 2.

This hypothesis reverses the view of Malicky (1969b) that multisegmental DNOs and TOs preceded the evolution of PCOs, and that the most advanced lycaenids rely on PCOs alone with respect to myrmecophily. However, the comparative evidence from Riodinidae and Lycaenidae morphology renders Malicky's view unlikely.

A more complete picture of the evolutionary sequence that has led from myrmeco-xenous lycaenids only exhibiting passive protective characters to the Lycaeninae with their sophisticated mutualistic or parasitic ant-associations will only arise on the grounds of a more detailed knowledge of the interactions between more ancestral ly-caenid caterpillars and ants, the morphology and histology of their epidermal organs, and the chemical composition of the secretions of PCOs and other setae. Overall, a more thorough phylogenetic approach is highly desired.

Specializations and reductions

Obligatory myrmecophily

While the primary steps in the evolution of lycaenid myrmecophily could only roughly be outlined above, the specializations and reductions that have further occurred can be discussed in greater detail on the grounds of available comparative data.

The ant-associations of ancestral Lycaeninae were most likely unspecific and faculta-tive, as are the ant-relationships of most extant Lycaenidae, Riodinidae, as well as of most trophobiotic Homoptera. However, obligatory and specific ant-associations do occur in a number of lycaenid caterpillars, and the question arises as to when and how specific ant-associations have evolved in the Lycaenidae.

First, what selective advantages may accrue to an obligate and specific myrmecophile? Obligate myrmecophiles are able to enter into ant nests or may even be actively adopted. Living in ant nests surely provides the most pronounced protection against other larval enemies, although highly specialized parasitoid ichneumonids even manage to parasitize *Maculinea* caterpillars inside *Myrmica* nests (Thomas, pers. comm.).

In addition, larvae living in ant nests may utilize ant brood as food resource. However, since ants are most aggressive against intruders in and near their nests, myrmecophiles will only be tolerated there if they are either well integrated into their host colony (using appropriate signals), or if they possess effective protective devices against fatal attacks.

The majority of obligatorily myrmecophilous Lycaenidae in fact lives in ant nests at least during one stage of their development. Numerous Aphnaeini, Theclini and Polyommatini pupate, rest or diapause in ant nests, and host-specificity appears to be distinctly beneficial in these cases. Similarly, all species where the larvae feed on ant brood (e.g. *Liphyra, Acrodipsas, Maculinea, Lepidochrysops*) or receive ant-regurgita-tions (*Euliphyra, Spindasis, Shirozua, Maculinea*), maintain genus-specific relation-ships to ants at least, and most of them are suspected to use specific communication signals. So, inquilinism strongly selects for host-specificity in myrmecophilous ly-caenids.

A second possible benefit from specific ant-associations is a low risk of "accidental mortality". Generalized signals cannot be optimal for all ant species a larva potentially encounters. Accordingly, some caterpillars might be killed by ants despite their myrmecophilous adaptations, and anecdotal evidence as well as some experimental data (Malicky 1961, 1970b) suggest that such accidental mortality does occur.

This ecological risk is most pronounced with dominant and aggressive ant species, and this might select for specializations of the larval signals. Optimized communication between a lycaenid species and its ant partner, then, could yield an improved protection against enemies.

This hypothesis is supported by the experimental data of Pierce & Eastseal (1986) and Pierce et al. (1987): the protective benefits from ant-association in the obligate myrmecophile *Jalmenus evagoras* by far exceeded those in the facultative myrmecophile *Glaucopsyche lygdamus*. Specific associations may also yield more stable and predictable benefits when compared with facultative conditional mutualisms, where the actual protection arising for the trophobionts may depend strongly on population density, enemy pressure, or species of attendant ant (Bristow 1984, Cushman & Whitham 1989).

However, to specialize on one host ant genus or species is also associated with considerable costs. The survival of an obligate myrmecophile is entirely dependent on the availability of its host ant, and fluctuations in the abundance of the host or even local extinctions severely affect the fate of such specialized lycaenids. *Maculinea arion*, for example, became extinct within a few years after the populations of its host ant *Myrmica sabuleti* had strongly declined in southern England due to habitat deterioration (Thomas 1989).

Many more populations of this and other *Maculinea* species with a similar life-cycle are now in great danger of extinction (e.g. Elmes & Thomas 1987), the close association with specific ants strongly limiting the ability of such species to react to environmental changes.

As a rule, most lycaenids whose larvae have tight and specific associations with ants only occur in highly isolated and fragmented populations (e.g. Smiley et al. 1988), or they do exist even in single colonies in an extremely limited area (e.g. many Aphnaeini and *Lepidochrysops* species in Africa: Henning 1984a, 1987b; *Acrodipsas illidgei, Paralucia pyrodiscus* in Australia: Samson 1987, 1989, Braby 1990).

Furthermore, obligate myrmecophiles may become unattractive to, or may even be attacked by, non-host ant species if the latter take the specific signals (pheromone mimics) of the caterpillars as an indication for the presence of competing and hostile alien ants. Samson & O'Brien (1980) and Pierce (1989) have reported that *Ogyris* and *Jalmenus* caterpillars are preyed upon by ants other than their usual hosts (see also Malicky 1961).

Accordingly, specific ant-associations should be less advantageous in areas with a highly diverse ant fauna, where the predictability to encounter the particular host ant taxon is low, whereas the risk of being preyed upon by inadequate non-host ants is high.

Obligatorily myrmecophilous lycaenids may further face with severe nutritional constraints. In obligate mutualisms there is a distinct selective pressure towards extremely high food rewards for attendant ants. *Anthene emolus* caterpillars exhibit extraordinarily high DNO secretion rates (Fiedler & Maschwitz 1989b; see also the permanent exudation of DNO secretions in some Aphnaeini), and in *Jalmenus evagoras* ant-attendance results in lower pupal weight and fecundity (Pierce et al. 1987, Elgar & Pierce 1988).

As a consequence the quality of larval nutrition achieves paramount importance (Baylis & Pierce 1991), and any shortage of food may become critical for the maintainance of ant-associations and hence for survival. Thus, less favourable or unpredictable food resources of lycaenid caterpillars may select against the evolution of obligate mutualisms. And secondly, if ants are used as oviposition cues, this either leads to a distinct reduction of the proportion of potential hostplants that can actually be utilized, or it forces the caterpillars to accept a wide array of plant species (Pierce & Elgar 1985).

So, physiological limitations in the potential to evolve polyphagy could pose severe constraints against those obligatory ant-associations that are based on large amounts of nutritive liquids.

Obligate and tight ant-associations are thus by no means generally advantageous when compared with facultative mutualisms, and one can formulate the following criteria for the evolution of obligate and specific myrmecophily in the Lycaenidae:

1.) Ecologically dominant ant species with highly predictable occurrence (e.g. long-lived colonies) are the preferred hosts.

2.) Obligate myrmecophily normally arises in lycaenid taxa whose larvae search shelter in ant nests for roosting, pupation or diapause.

3.) A permanently high enemy pressure reinforces the evolution of obligate associations.

4.) Caterpillars that prey upon ant brood always need (and have) specific host ants.

As a corollary conditions can be exemplified where obligatory myrmecophily should rarely evolve:

1.) Rare ant species or ants with very small colonies are unlikely hosts of obligate myrmecophiles.

2.) Regions with a depauperate ant fauna (islands, high latitudes or altitudes) rarely house obligatorily myrmecophilous lycaenids.

3.) In tropical rainforests with their extremely diverse ant fauna relatively fewer obligate myrmecophiles are expected, since there the predictability of finding the adequate hosts is lower.

4.) Widely distributed lycaenids, or species occurring in a broad range of ecological conditions, have a low likelihood of specializing towards one particular host ant.

These criteria could partly explain the zoogeographical pattern that obligate myrmecophily is common in Australia and South Africa, less common in the wet tropics and rather rare in the temperate regions. Tropical rain forests with their extraordinarily diverse ant fauna (Hölldobler & Wilson 1990) provide rather few trophobiotic ant species whose occurrence is sufficiently predictable to support the evolution of obligate myrmecophily.

One of the few exceptions is the dominant genus *Oecophylla*, and this ant indeed houses several obligatorily myrmecophilous lycaenids. In contrast, the risk of en-

countering inadequate hostile ants, or the risk not to find the appropriate combination of hostplants and host ants, is rather high in these most species-rich terrestrial habitats.

In subtropical, seasonally dry habitats a less diverse ant fauna with distinctly dominant species exists. Likewise, the flora is less diverse with some species dominating the vegetation. In such areas lycaenid caterpillars derive considerable protection and microclimatic benefits from visiting ant nests during day time or dry seasons, and the enemy pressure during the short active period of larvae must be considered to be rather high (see Pierce et al. 1987 for an Australian species).

All these factors, in concert, should have promoted the evolution of obligate ant-associations, and in fact the highest proportions of obligate myrmecophiles occur in areas matching the above conditions (Australia and South Africa). Once such an association has been established, the fragmentation and isolation of the populations may subsequently lead to speciation, and the large species diversity of the Aphnaeini genera *Spindasis, Aloeides*, and *Poecilmitis*, or of the polyommatine genus *Lepidochrysops* undoubtedly evolved in this way.

In temperate zones (e.g. Holarctic region), obligate associations are rather rare. The generally lower diversity of ants and lycaenids, the presumably lower selective pressure exerted by parasitoids and predators, the often highly fluctuating and unpredictable climatic conditions, and the restricted activity periods of lycaenids and ants obviously did not favour the evolution of specific and obligate associations in a greater number of species.

Clearly the evolution of obligate myrmecophily has also a historical and taxonomical dimension. Historically, the evolution of obligate symbioses requires sufficient time to allow the accumulation of the adaptations required. The extermination of large parts of the Holarctic lycaenid fauna due to repeated glaciations has certainly restricted or cut off the evolution of more numerous obligatory ant-associations. In tropical and subtropical regions, in contrast, evolution was not as totally interrupted, albeit considerable climatic deteriorations have occurred there as well.

Taxonomically, the rise of obligate ant-associations is restricted to certain subgroups of the Lycaenidae (this study), and this has two possible reasons. First, the potential to evolve specific ant-associations is not equally available in all taxa. For example, secondarily myrmecoxenous lycaenids, which have reduced or lost their ant-organs and ant-associations, are less likely to evolve specific myrmecophily again (Thecliti, Lycaenini).

Secondly, once a lycaenid species has attained obligate myrmecophily, it is likely that its phylogenetic descendents retain or further modify this character. As with the hostplant relationships, a distinct phyletic conservatism must be expected.

The mechanisms engaged in obligatory myrmecophily (recognition of host ants, production of specific chemicals) further pose distinct barriers against random shifts in the host ants used. Accordingly, whole genera can be characterized by their obligate myrmecophily, and all more or less subtle specific differences regarding myrmecophily within these genera must be viewed as secondary adaptations during speciation (e.g. *Spindasis, Phasis, Poecilmitis, Acrodipsas, Maculinea, Lepidochrysops*).

In other genera (e.g. *Aloeides, Hypochrysops, Ogyris, Jalmenus*), the evolution of obligate myrmecophily seems to have occurred in parallel several times starting from similar preconditions (steadily myrmecophilous larvae), but this view may well be modified if more is known about the phylogeny and behavioural ecology of the respective taxa.

Interestingly, there is yet no evidence that a reverse evolution from obligatory towards facultative myrmecophily has ever occurred within the Lycaenidae, although such would be possible from theory. Apparently, obligate myrmecophily is mostly an evolutionary "one-way road" leading to ever increasing specialization, and it has been followed by a rather limited number of lycaenid genera. Only a few of these were distinctly successful in terms of species number, area of distribution, or abundance in their habitats, while in other lineages the obligatory myrmecophiles remained a small minority.

To the end of this discussion of obligate myrmecophily, some of the better known examples shall be shortly visited under an evolutionary view.

1.) Aphnaeini: As a whole this tribe is characterized by its tight relationships to ants, and a close association with *Crematogaster* (Myrmicinae) may well belong to its groundplan. Deviations occur in the monophyletic group *Aloeides/Erikssonia* (always associated with *Acantholepis* [Formicinae]) and in *Axiocerses amanga* and *Poecilmitis pyroeis* (with *Camponotus* [Formicinae]). Records of *Spindasis* or *Axiocerses* with *Pheidole* require confirmation.

This implies that major host shifts (even across ant subfamilies) are possible, but they either occur only in single cases (*Axiocerses, Poecilmitis*), or they give rise to a new radiation (*Aloeides*). Clearly, the host ant relationships of obligatorily myrmecophilous lycaenids are not basically coincidental, but largely follow phyletic patterns.

2.) Luciiti: Tight relationships to the ant genus *Iridomyrmex* (Dolichoderinae) are characteristic for this subtribe. Primarily these associations were probably not obligatory (as it is still the case with *Pseudodipsas* or several *Hypochrysops* species), and a few *Hypochrysops* species and the *Philiris* lineage of the *Hypochrysops* section have even reduced this myrmecophily. *Lucia, Paralucia, Acrodipsas*, and several *Hypochrysops* species have evolved obligate ant-associations in parallel.

Again major host shifts across ant subfamilies have occurred (to *Notoncus* [Formicinae] and at least twice to *Crematogaster* [Myrmicinae]), even within the genus *Acrodipsas* whose larvae are predators of ant-brood. Nevertheless, obligate myrmecophily and host ant use in the Luciiti show a distinct taxonomic pattern.

3.) *Ogyris* and *Jalmenus*: Judging from the data given by Atsatt (1981b) and Common & Waterhouse (1981) some *Ogyris* species are facultatively myrmecophilous and largely associated with Dolichoderinae ants (*Iridomyrmex, Froggatella, Technomyrmex*), including at least one obligatorily myrmecophilous species, *Ogyris amaryllis*. Another group of species is associated with the Formicinae genus *Camponotus*, again containing some obligate myrmecophiles.

It is not yet known whether this pattern, starting from facultative associations, is due to an early dichotomy towards *Camponotus* or *Iridomyrmex* as host ants, or whether first obligate myrmecophily evolved, followed by a later shift in the host ant genus utilized.

The genus group *Jalmenus/Pseudalmenus* is associated with Dolichoderinae ants (mainly *Iridomyrmex*, also *Froggatella*), suggesting an ancestral adaptation to this peculiar ant group. Several species have, perhaps independently, transcended the stage of steady, but facultative myrmecophily and now maintain obligate mutualisms.

4.) *Maculinea*: This small genus of the *Glaucopsyche* section is closely related to *Iolana* and *Glaucopsyche*. The latter, in particular, is highly myrmecophilous with species from the genus *Myrmica* among its attendant ants. *Glaucopsyche* larvae sometimes pupate in ant nests (Tilden 1947). It seems feasible that the *Glaucopsyche*-like ancestor of today *Maculinea* first regularly entered into ant nests for pupation and diapause. Then, probably, a shift from pupal (typical for species of the *Glaucopsyche* section) to larval diapause occurred.

Since *Myrmica* is one of the few Holarctic ant genera that have brood throughout the year, only larvae hibernating in colonies of this genus could additionally use ant grubs as food resource, perhaps in response to shortages in plant food (climatic constraints during the ice ages?). This selected for a specialization upon *Myrmica* ants as hosts with the evolution of the associated adoption and integration mechanisms.

Finally, the most advanced species (*M. alcon, M. rebeli*) even shifted from brood predation to solicitation of trophallactic regurgitations, thus more effectively utilizing the ant colonies as food resource.

5.) *Lepidochrysops*: The closest relatives of this genus are the mainly African *Euchrysops* species that are facultatively myrmecophilous. *Camponotus* ants are well represented among the attendant ants of *Euchrysops* larvae, and *Eu. dolorosa* appears to be somewhat specialized to *Camponotus niveosetosus* chemically (Henning 1983b). In *Lepidochrysops*, *Camponotus* became the exclusive host ants. Some species usually referred to as *Lepidochrysops* (*lacrimosa, ariadne*?) are still facultative myrmecophiles with entirely herbivorous larvae (Clark & Dickson 1971).

The remaining species shifted to Lamiaceae/Selaginaceae (with few secondary extensions) and became brood predators of two peculiar *Camponotus* species. As within the *Maculinea-Glaucopsyche* group the larval period of these *Lepidochrysops* species is distinctly longer than in their phytophagous relatives. This suggests that again a shift towards larval diapause in ant nests (perhaps as a response to escape dry seasons?) may have been a decisive step in the evolution of carnivory in the *Lepidochrysops* section.

Secondary myrmecoxeny

Reductions of myrmecophily have repeatedly occurred, and most of these instances can be related to three factors: larval hostplants, feeding habits, and habitat. While apparently none of these factors is alone suffcient to favour secondary myrmecoxeny, a combined incidence of two or more of them has obviously selected against ant-associations.

H o s t p l a n t s — As has been discussed above, myrmecoxeny largely occurs in ly-caenids whose larvae are food specialists on, for lycaenid larvae, "unusual" hostplants. *Philiris* on Lauraceae, Moraceae, or Euphorbiaceae, Thecliti on Hamamelididae or Oleaceae, *Eumaeus* on cycads, or *Agriades* on Primulaceae provide examples. Possibly, the association of Lycaenini caterpillars with Polygonaceae (that often contain high amounts of oxalic acid) have also played a role in the loss of true myrmecophily.

Such hostplants may be nutritionally inferior, although ant-associations are known from other lycaenids feeding on the same plant taxa. Furthermore, the myrmecoxenous food specialists may derive some protection from secondary plant compounds that render them unpalatable for predators (proven for *Eumaeus*: Bowers & Larin 1989, Bowers & Farley 1990; feeding experiments with *Lycaena tityrus* larvae offered to *Leptogenys* and *Pseudomyrmex* ants also suggest unpalatability: Fiedler, unpublished).

Generally, the comparative survey of more than 1000 lycaenid species supports the notion that specific associations with deviating hostplants favour reductions of myrmecophily, albeit this trait is by far not universal.

F e e d i n g h a b i t s — Caterpillars with endophytic life-habits (e.g. fruit-borers) are often myrmecoxenous. At a first stage the development of the TOs is delayed (*Leptotes*), or they are completely reduced (*Cupido, Iolana, Deudorix, Capys*, Hypolycaeniti, Eumaeiti). Reductions of the TOs are likewise common in species whose larvae live in ant nests (*Acrodipsas, Maculinea, Lepidochrysops*), suggesting that the function of these organs becomes insignificant in hollow spaces and cavities.

As a next step the DNO may be totally reduced (*Artipe, Bindahara, Cacyreus*). Typically, flower- or fruit-boring lycaenid larvae are rarely or never visited by ants. Endophytism thus proves a well-founded alternative defence strategy that partly renders myrmecophily superfluous. However, several endophytic larvae still retain a DNO and at least weak ant-associations (e.g. *Hypolycaena, Leptomyrina, Deudorix, Everes* etc.).

H a b i t a t — Habitats with a depauperate ant-fauna favour secondary myrmecoxeny. The Hawaii islands have no native ant species, and the endemic *Udara blackburni* (Polyommatini) has in fact neither a DNO nor TOs (Scott 1986). Most Thecliti mainly occur in the canopy of temperate zone deciduous forests, and Jeanne (1979), Fellers (1987, 1989) and Weseloh (1989) have provided evidence that the selective pressure arising from predatory ants is distinctly lowered in such habitats.

A reduced abundance and diversity of ants implies a lower chance of maintaining stable ant-associations and its related potential benefits, and it thus may have supported the loss of ant-organs in the ancestor of the subtribe Thecliti.

The ant-fauna of arctic or alpine tundras is extremely impoverished, and unsurprisingly several lycaenids specialized to these habitats are secondarily myrmecoxenous (*Agriades, Vacciniina optilete*). A similar altitudinal trend was noted for ant-associations of membracids (Olmstead & Wood 1990b).

In summary, judging from a global survey of life-histories, certain traits select against the maintenance of ant-associations, although none of these is at the same time

necessary and sufficient. In various taxa the mechanisms selecting for secondary myrmecoxeny are not even marginally understood (e.g. Lycaenini).

The lability of lycaenid myrmecophily in evolutionary time is perhaps less pronounced than previously postulated (e.g. Kitching & Luke 1985, Pierce 1987), but certainly the local selective "environment" of a given caterpillar species is ultimately decisive as to whether the benefits of myrmecophily outweigh its costs.

A more detailed understanding of the selective forces favouring secondary myrmecoxeny requires a more complete knowledge of the respective species, and clearly the study of lycaenid myrmecophily will decidedly profit from investigations that include myrmecoxenous caterpillars.

Species diversity of the Lycaenidae: is myrmecophily a part of the answer?

It has repeatedly been suspected that the relationships between lycaenids and ants have supported the radiation of the former (e.g. Ehrlich & Raven 1964, Vane-Wright 1978, Cottrell 1984), but only one study has attempted to exemplify how ant-associations could amplify the species diversity (Pierce 1984). She suggested two possible scenarios:

a) If lycaenid females oviposit in the presence of specific host ants, "oviposition mistakes" on non-hostplants may occur more often than in other butterflies only responding to plant chemistry when egg-laying. Although most such oviposition mistakes do not result in a successful amplification of the hostplant range, at least a few cases will do so. Given the postulated greater absolute frequency of these mistakes in lycaenids, there should exist a significant potential pathway towards adaptation to new hostplants and diversification, eventually resulting in speciation.

b) If lycaenids require a combination of both specific host ants and food plants, their populations should occur more patchily than in most other butterflies. Accordingly, the isolation of such demes more likely favours speciation, even more so since most lycaenids are not migratory.

Available evidence supports both hypotheses. At least some species lay eggs on a broad range of plants merely in the presence of appropriate ants, and many closely ant-associated species have extremely fragmented populations (e.g. Pierce 1984, Henning 1987b, Elmes & Thomas 1987, Smiley et al. 1988). However, ant-dependent oviposition is restricted to, but is not even universal among, obligatory myrmecophiles, and the majority of obligatorily myrmecophilous lycaenids are food specialists (see above).

Furthermore, a combination of specific hostplants and host ants is again only important for obligate myrmecophiles, and evidence has been presented above that these probably account for less than 20 % of the extant species diversity of the Lycaenidae. So, albeit the two scenarios presented by Pierce (1984) hold true for some specialized lycaenid groups, they cannot generally explain the great diversification of this family.

Further objections additionally qualify the general validity of both hypotheses. As already emphasized by Chew & Robbins (1984), the widest hostplant ranges are observed in lycaenids that are specialized on flowers or fruits (see also this study). Probably,

egg-laying on immature plant tissues with presumably lower contents of secondary compounds increases both the likelihood of oviposition mistakes and the probability that the actual substrate can be consumed by the emerging larvae.

However, flower- and fruit-feeding is by no means restricted to highly myrmecoxenous caterpillars, but is indeed most widespread among caterpillars with low-level ant-associations. Especially some Eumaeiti genera (*Callophrys, Strymon*; see also Fiedler 1990d) heavily utilize flowers, and the hostplant ranges of these mostly myrmecoxenous genera are remarkable, including conifers and monocots.

Therefore, the hostplant diversification pathway via flower- or fruit-feeding is certainly a very important one for the evolution of the Lycaenidae, but it is by no means restricted to, or best developed among, obligatory myrmecophiles. Rather, there is a taxonomic pattern: this mechanism is most important in taxa with a distinct overall preference for inflorescences (e.g. Deudorigiti, Eumaeiti, Polyommatini), irrespective of myrmecophily.

Atsatt (1981b) and Pierce (1984) also stated that host shifts among food plants should be more easy to achieve via oviposition mistakes than shifts between host ants. The conservative association of numerous obligatory myrmecophilous genera with one host ant genus each (most Aphnaeini, *Lepidochrysops, Maculinea*) supports this view, but significant exceptions even across ant subfamilies do exist (*Hypochrysops, Acrodipsas, Poecilmitis*; see above). Thus, although certainly a rare event, successful major host ant shifts are possible.

With regard to the "speciation through fragmentation" scenario, it seems feasible that the high number of locally endemic species in African genera such as *Aloeides, Poecilmitis* and related Aphnaeini, or the species-diversity of *Lepidochrysops* have evolved as a consequence of extreme fragmentation of populations, and several of these taxa are known only from single colonies (Henning 1987b). A similar situation may be prevalent among some Australian Luciiti or Zesiiti.

Populations of the Holarctic *Plebejus idas* (specifically associated with certain *Formica* ants) and of the Palaearctic *P. argus* (associated with *Lasius* species) are typically very localized, and these two species might diverge into new species in the course of evolution (both are yet subdivided in numerous morphologically distinct subspecies).

Other obligate myrmecophiles, however, have huge distributions. Several *Maculinea* species occur through large parts of the Palaearctic region (*M. arion, M. teleius, M. alcon*), but there is little evidence that their localized populations (that are often referred to as "subspecies") differ more markedly than populations of non-myrmecophilous species covering a comparable range. *Liphyra brassolis* occurs from India to Australia with only minor geographic variation.

Furthermore, highly localized popualtions exist in many facultatively myrmecophilous and myrmecoxenous species. The subgenus *Agrodiaetus* in the *Polyommatus* group offers an excellent example of an explosive radiation in the circum-Mediterranean region and West Asia. Typically, *Agrodiaetus* taxa differ little except in chromosome numbers.

Another example for highly fragmented allopatric population groups is provided by the Eurasiatic subgenus *Plebejides* (Bálint & Kertész 1990). Both *Agrodiaetus* and *Plebejides* are closely, but unspecifically associated with ants, and there is no evidence that factors other than historical changes in the climate and availability of hostplants have promoted isolation and speciation (see Bálint 1991 for *Plebejides*). Examples of myrmecoxenous lycaenids with isolated and fragmented populations in parts of their distribution area are *Lycaena helle* and *L. dispar*.

Thus, fragmentation of populations, geographical isolation, and subsequent (not necessarily allopatric) specialization to novel hostplants are the most important speciation processes among myrmecoxenous and facultatively myrmecophilous lycaenids, as well as among obligate myrmecophiles. In the latter, fragmentation may be enhanced, and hostplant changes might occur more often in certain subgroups in response to specific ant-associations, as suggested by Pierce (1984).

Given the restricted number of obligate myrmecophiles, these processes can at best explain the evolution of species diversity in taxa such as Aphnaeini, Luciiti, Zesiiti, or the *Lepidochrysops* section. For the remaining majority of the extant Lycaenidae, there is at present no evidence that and how ant-associations could have promoted speciation directly.

The impressive species-richness of the Lycaenidae as a whole suggests that myrmecophily has indeed played an important role. Most likely, the generalized notion that ant-association offers an important adaptive zone ("enemy-free space") with limited competition of related herbivores (i.e. other butterfly caterpillars), in combination with higher survival rates of myrmecophilous larvae, are sufficient explanations for the evolutionary success of the Lycaenidae. In terms of hostplant specializations and total species diversity, the Nymphalidae have distinctly overtaken the Lycaenidae.

Concluding remarks

The present study is an attempt to combine experimental and life-history data with morphological, systematic, zoogeographical and ecological traits. Besides making accessible the scattered information on more than 1000 lycaenid species, it was intended to demonstrate that comparative methods combined with attempts to understand the phylogeny are crucial to achieve a more detailed view of evolution.

Experimental data and theoretical considerations strongly require to be supplemented from the fund of organismic and descriptive biology. Unfortunately, the phylogeny of the Lycaenidae is not yet sufficiently worked out to allow more rigid quantitative analyses and predictions (cf. Harvey & Purvis 1991). However, since the comparative method has generally turned out to yield significant results even if the underlying phylogeny is not completely resolved, the hypotheses discussed here should provide a reasonable basis for further studies.

The ant-associations of the Lycaenidae are perhaps the best-known paradigm of myrmecophilous interactions, and continued investigations seem especially rewarding.

The documentation of further life-history data of today under-represented taxa (especially from the tropics), the sampling of additional experimental data on the chemistry of myrmecophilous secretions and on the details of behavioural interactions, and, with high priority, a more complete phylogenetic analysis must now continue. Then, a synthesis of classical biology, experimental ethology and ecology, and theoretical sociobiology and evolutionary biology will be attained.

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APPENDIX: TABLES 17-19

Table 17: This table summarizes all information traced concerning larval food substrates, host-range indices, preferences for protein-rich hostplant tissues, and data regarding the presence of myrmecophilous organs and/or ant-associations for more than 1000 lycaenid species.

First column: Species arranged according to the higher classification adopted throughout this work. Nomenclature and taxonomy largely follow Bridges (1988), but deviate where more recent revisions are available. When the original records were published under a different species name (synonyms, misidentifications), this name is included in brackets in selected cases. Generic synonymies are omitted. Subspecies are generally not considered except a few cases where the taxonomic status is uncertain. Subgenera are given to facilitate use, if these are regularly treated as distinct genera as well.

Second column: Hostplant families (according to Ehrendorfer 1983), or other food substrates used by larvae. The first entry is usually the main hostplant taxon. The subsequent plant families are arranged in systematic order, the sequence not implying any preference hierarchies. In polyphagous species the listing starts with the legume families where appropriate. Question-able records are indicated by ?, highly doubtful data by ??. Where obvious from the sour-ces, laboratory data are designated with **lab**. Oviposition records (**ov.**) are only included when the respective substrate is likely to be the larval food.

Third column: Host-range indices. **1** : monophagous (1 hostplant species); **2** : stenoligo-phagous (1 hostplant genus); **3** : oligophagous (1 hostplant family); **4** : moderately polyphagous (2 hostplant families); **5** : polyphagous (3+ hostplant families). Very closely related plant families are treated as one taxon for these indices (e.g. the legume families Mimosaceae, Caesalpini-aceae and Fabaceae; Lamiaceae and Selaginaceae). Tentative assignments are followed by ?. Entirely non-herbivorous species (e.g. Liptenini, Miletinae) are excludeded (-). A question mark ? alone indicates that, based on the literature evaluated, no categorization is possible at present.

Fourth column: Preferences for presumed protein-rich hostplant parts. **y** : preference for young growth/buds; **i** : preference for inflorescences; **f** : preference for fruits or seed capsules; **e** : larvae with (at least partially) endophytic life-habits. – : no such preferences recorded. Assignments in parentheses () are hypothetically derived from closely related species. A question mark ? indicates that, based on the literature evaluated, no categorization is possible at present.

Fifth column: Degree of myrmecophily (as defined in Fiedler 1991) and presence of myr-mecophilous organs. All records refer to older larvae except where stated otherwise. **0** : myrmecoxenous (not associated with ants in the field); **1** : weakly myrmecophilous (only casual and instable ant-associations); **2** : moderately myrmecophilous (ant-associations regularly occur at least with part of the larvae); **3** : steadily myrmecophilous (almost all older larvae are nearly permanently attended by ants); **4** : obligatorily myrmecophilous (caterpillars are dependent on ants: obligatorily mutualistic or parasitic larvae). ** : larvae with DNO and TOs present; * : only DNO present; ^{T} : only TOs present; no symbol: only PCOs. Symbols in parentheses () refer to hypothetical assignments based on closely related species. Doubtful data are followed by ?. A question mark ? alone indicates that, based on the literature evaluated, no categorization is possible at present.

Sixth column: Selected references. A full bibliography would have been impossible, es-pecially for many Holarctic species.

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Poritiinae:					
Poritiini:					
Poritia erycinoides	Fagaceae	2?	?	0	Rosier 1951
Liptenini:					
Pentiliti					
Alaena amazoula	Lichen	–	–	0	Migdoll 1988
A. margaritacea	Lichen	–	–	0	Clark & Dickson 1971
A. nyassa	Lichen (ov.) Poaceae ??	–	–	(0)	Kielland 1990, Ackery & Rajan 1990
A. caissa	Lichen ?	–	–	(0)	Kielland 1990
A. subrubra	Anacardiaceae ??	–	–	(0)	Ackery & Rajan 1990
Pentila tropicalis	Lichen	–	–	0	Migdoll 1988
P. inconspicua	Lichen ?	–	–	(0)	Kielland 1990
P. rogersi	Lichen ?	–	–	(0)	Kielland 1990
P. rondo	Lichen ?	–	–	(0)	Kielland 1990
Telipna erica consanguinea	Lichen	–	–	0	Jackson 1937
T. sanguinea	Lichen	–	–	0	Jackson 1937
Ornipholidotos muhata	Lichen	–	–	0	Jackson 1937, van Someren 1974
Durbaniiti					
Durbania amakosa	Cyanobacteria	–	–	0	Henning 1983a
D. limbata	Lichen	–	–	0	Migdoll 1988
D. saga	Lichen	–	–	0	Clark & Dickson 1971
Cooksonia neavei	Lichen	–	–	0	Pennington et al. 1978
C. aliciae	Lichen	–	–	0	Ackery & Rajan 1990
Lipteniti					
Mimacraea krausei	Lichen	–	–	0	Jackson 1937
M. marshalli	Lichen	–	–	0	Stempffer 1967
M. skoptoles	Lichen (ov.)	–	–	(0)	Kielland 1990
M. poultoni	Lichen	–	–	(0)	van Someren 1974
Citrinophila tenera	Lichen ?	–	–	0	Farquharson 1922
C. erastus	Lichen ?	–	–	(0)	Kielland 1990
Teriomima zuluana	Lichen	–	–	0	Migdoll 1988
T. micra	Lichen (ov.)	–	–	(0)	Kielland 1990
T. subpunctata	Lichen (ov.)	–	–	(0)	van Someren 1974
T. parva	Lichen (ov.)	–	–	(0)	Kielland 1990
Euthecta cooksoni	Lichen (ov.)	–	–	(0)	Kielland 1990
Baliochila aslauga	Lichen Fabaceae ??	–	–	0	Migdoll 1988
B. hildegarda	Lichen	–	–	0	Sevastopulo 1975
B. dubiosa	Lichen (ov.)	–	–	(0)	van Someren 1974
B. fragilis	Lichen (ov.)	–	–	(0)	van Someren 1974
B. minima	Lichen (ov.)	–	–	(0)	van Someren 1974
B. stygia	Lichen (ov.)	–	–	(0)	van Someren 1974
Cnodontes vansomereni	Lichen (ov.)	–	–	(0)	Kielland 1990

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Eresina corynetes	Lichen ?	–	–	0	Farquharson 1922
Eresinopsides bichroma	Lichen ?	–	–	(0)	Kielland 1990
Mimeresia libentina	Lichen (ov.)	–	–	(0)	Ackery & Rajan 1990
Liptena undina	Lichen	–	–	0/4?	Jackson 1937
Teratoneura isabellae	Lichen	–	–	0/4?	Farquharson 1922
Iridana incredibilis	Lichen	–	–	0	Jackson 1937
I. perdita marina	Lichen	–	–	0/4?	Jackson 1937
Deloneura millari	Lichen ?	–	–	0	Migdoll 1988
+ ssp. *sheppardi*	Lichen ? Fabaceae ??	–	–	0	Clark & Dickson 1971
D. ochrascens	Lichen (ov.)	–	–	0/4??	Jackson 1937, van Someren 1974, Kielland 1990
D. subfusca	Lichen ?	–	–	(0?)	Kielland 1990
Epitola (Aethiopana) honorius	Lichen	–	–	3?	Farquharson 1922
E. (Epitola) concepcion	Lichen	–	–	0	Farquharson 1922
E. hewitsoni	Lichen	–	–	0	Farquharson 1922
E. miranda	Lichen	–	–	0	Farquharson 1922
E. urania	Lichen	–	–	0/3?	Jackson 1957
E. carcina	Lichen ?	–	–	3?	Ackery & Rajan 1990
E. catuna	Lichen	–	–	3	van Someren 1974
E. ceraunia	Lichen ?	–	–	3?	Ackery & Rajan 1990
E. cercene	Lichen	–	–	3	van Someren 1974
E. elissa	Lichen ?	–	–	3?	Ackery & Rajan 1990
E. kamengensis	Lichen	–	–	3	van Someren 1974
Hewitsonia similis	Lichen	–	–	0	Farquharson 1922
H. kirbyi	Lichen	–	–	0	Jackson 1937
H. crippsi	Lichen ?	–	–	0	Jackson 1947
Miletinae: **Miletini:** **Spalgiti**					
Spalgis epeus	Coccidae	–	–	0	Cottrell 1984
Sp. lemolea	Coccidae Pseudococcidae	–	–	0	Cottrell 1984
Feniseca tarquinius	Pemphigidae	–	–	0	Scott 1986, Klassen et al. 1989
Tarakiti					
Taraka hamada	Hormaphididae + honeydew + siphon secretions	–	–	0	Cottrell 1984, Banno 1990
Miletiti					
Miletus chinensis	Aphidoidea	–	–	0/3?	Cottrell 1984
M. boisduvali	Aphidoidea Coccidae	–	–	0/3?	Cottrell 1984

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Miletus biggsii	Hormaphididae Coccidae	–	–	0/4?	Maschwitz et al. 1988
M. symethus	Coccidae *Dolichoderus* brood ?	–	–	0/4?	Eliot 1980
M. nymphis	Coccidae	–	–	(0/3?)	Maschwitz et al. 1988
Allotinus unicolor	Hormaphididae Psyllidae ? Membracidae ?	–	–	0/3?	Maschwitz et al. 1985a, Fiedler & Maschwitz 1989c
A. subviolaceus	Membracidae	–	–	0	Maschwitz et al. 1985a
A. major	Membracidae	–	–	0	Kitching 1987
A. davidis	Aphidoidea	–	–	0	Maschwitz et al. 1985a
A. substrigosus	Hormaphididae	–	–	0	Maschwitz et al. 1988, Schütze 1990
A. apries	Coccidae (L1) *Myrmicaria* brood ?	–	–	4?	Maschwitz et al. 1988
Logania malayica	Hormaphididae ?	–	–	0?	Maschwitz et al. 1988
Megalopalpus zymna	Membracidae Jassidae	–	–	0	Cottrell 1984
Lachnocnemiti					
Lachnocnema bibulus	Jassidae Membracidae Psyllidae + honeydew + *Camponotus* regurgitations	–	–	0/4?	Cripps & Jackson 1940, van Someren 1974, Cottrell 1984
L. brimo	Membracidae Psyllidae	–	–	0?	Ackery 1990
L. durbani	Coccidae (lab) Membracidae (lab)	–	–	0?	Ackery & Rajan 1990
Thestor dicksoni	*Anoplolepis* brood ?	–	–	4	Clark & Dickson 1971
Th. basutus	Psyllidae (L1–L3) *Anoplolepis* brood ?	–	–	4	Clark & Dickson 1971
Th. obscurus	Ant brood ?	–	–	4?	Claassens & Dickson 1980
Th. brachycerus	Ant brood ?	–	–	(4?)	Clark & Dickson 1971
Th. dukei	Ant brood ?	–	–	(4?)	Clark & Dickson 1971
Th. rileyi	Ant brood ?	–	–	(4?)	Clark & Dickson 1971
Th. holmesi	Ant brood ?	–	–	4	Clark & Dickson 1971
Th. protumnus	Coccidae Ant brood ?	–	–	(4?)	Clark & Dickson 1971, Migdoll 1988
Liphyrini:					
Euliphyra mirifica	*Oecophylla* regurgitations + prey items of host ants	–	–	4	Hinton 1951, Dejean 1991
Eu. leucyania	*Oecophylla* regurgitations + prey items of host ants	–	–	4	Kielland 1990, Dejean 1991
Liphyra brassolis	*Oecophylla* brood	–	–	4	Johnson & Valentine 1986, Cottrell 1987
Aslauga lamborni	Membracidae Coccidae	–	–	0^T	van Someren 1974, Cottrell 1984
A. purpurascens	Membracidae Psyllidae (lab) Coccidae (lab)	–	–	0^T	Boulard 1968, Cottrell 1981

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Aslauga latifurca	Membracidae Coccidae Lycaenidae (lab)	-		$0?^T$	Jackson 1937, Cottrell 1981, Ackery & Rajan 1990
A. atrophifurca	Homoptera	-	-	$0^{T?}$	Cottrell 1984, Villet 1986
A. orientalis	Coccidae	-	-	(0^T)	Cottrell 1981
A. vininga	Coccidae Pseudococcidae	-	-	$0?^{(T)}$	Cottrell 1984, Ackery & Rajan 1990
Curetinae:					
Curetis thetis	Fabaceae Meliaceae	4	y, i	0^T	Hinton 1951
C. regula	Fabales	3?	y	$0/2?^T$	DeVries 1984
C. felderi	Fabaceae	3	y	0^T	pers. obs.
C. santana	Fabaceae	3	(y, i)	0^T	Corbet & Pendlebury 1978
C. bulis	Fabaceae	3?	y	0^T	Eliot 1980
C. acuta	Fabaceae	3	(y)	0^T	Iwase 1954, Shirôzu & Hara 1974
+ ssp. *dentata*	Fabaceae	3	y	$(0)^T$	Johnston & Johnston 1980
Lycaeninae: Aphnaeini:					
Aphnaeus erikssoni	Convolvulaceae	2?	?	(4**)	Sevastopulo 1975
A. argyrocyclus	Euphorbiaceae	1?	?	(4**)	Sevastopulo 1975
A. orcas	Euphorbiaceae Mimosaceae Loranthaceae	5	?	(4**)	Sevastopulo 1975, Ackery & Rajan 1990
A. (Paraphnaeus) hutchinsoni	Loranthaceae upon Mimosaceae	2/4?	e (galls)	4**	Jackson 1937, van Someren 1974
Spindasis ella	Mimosaceae Fabaceae	3	e	3/4**	Clark & Dickson 1971
S. homeyeri	Mimosaceae Caesalpiniaceae	3	?	(3/4**)	Sevastopulo 1975, Pennington et al. 1978
S. natalensis	Fabaceae Rubiaceae Verbenaceae Olacaceae ?	5	e	4**	Clark & Dickson 1971, Sevastopulo 1975
S. victoriae	Mimosaceae	3	y	(3/4**)	Pennington et al. 1978
S. mozambica	Fabaceae	3	?	(3/4**)	Sevastopulo 1975
S. nyassae	Mimosaceae Fabaceae + *Crematogaster* regurgitations ?	3	y	4**	Hinton 1951, Sevastopulo 1975
S. avriko	Mimosaceae	2?	y, e (galls)	4(**)	Ackery & Rajan 1990
S. tavetensis	Mimosaceae	2?	y, e (galls)	4(**)	Ackery & Rajan 1990
S. apelles (+ ssp. *nairobiensis*)	Anacardiaceae (ov)	2?	?	(4**)	van Someren 1974, Sevastopulo 1975
S. namaqua	Zygophyllaceae	2	?	4**	Henning 1983a
S. phanes	Olacaceae	2	?	4**	Henning 1983a

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Spindasis lohita	Mimosaceae Proteaceae Myrtaceae Combretaceae, Santalaceae, Loranthaceae, Convolvulaceae, Dioscoreaceae	5	?	3/4**	Corbet & Pendlebury 1978
S. vulcanus	Rutaceae Sapindaceae Rhamnaceae Rubiaceae Verbenaceae	5	?	3/4**	Pierce & Elgar 1985
S. takanonis	Pinaceae Rosaceae Elaeagnaceae + *Crematogaster* regurgitations	5	?	4**	Iwase 1955, Pierce & Elgar 1985
Cigaritis zohra	Fabaceae	1	–	4**	Thomas & Mallorie 1985, Rojo de la Paz 1990
C. allardi	Fabaceae Cistaceae	4	–	3**	Thomas & Mallorie 1985, Rojo de la Paz 1990
C. siphax	Cistaceae ??	?	?	(3/4**)	Devarenne 1990
C. (Apharitis) myrmecophila	Polygonaceae	1?	?	4**	Hinton 1951
C. (A.) acamas	Caesalpiniaceae ? Fabaceae ? + *Crematogaster* regurgitations, + *Crematogaster* brood ?	3?	?	4**	Larsen & Pittaway 1982
Axiocerses tjoane	Mimosaceae	2	?	(4**)	Migdoll 1988
A. bambana (ssp.?)	Mimosaceae	3	?	4**	Clark & Dickson 1971
A. amanga	Olacaceae Mimosaceae	4	–	3**	Jackson 1937, Sevastopulo 1975
A. harpax	Mimosaceae + *Crematogaster* regurgitations ?	2?	e (galls)	4**	Jackson 1947, Ackery & Rajan 1990
A. styx	Caesalpiniaceae	2?	?	(3**)	Sevastopulo 1975
A. (Desmolycaena) mazoensis	Mimosaceae	2	i	(3**)	Migdoll 1988
A. (Chloroselas) pseudozeritis	Mimosaceae + *Crematogaster* regurgitations ?	2	y	4**	Jackson 1937, van Someren 1974
Crudaria leroma	Mimosaceae	3	y	4**	Clark & Dickson 1971
Phasis thero	Anacardiaceae Melianthaceae (lab)	4	e	4^{T}	Clark & Dickson 1971
Ph. braueri	Anacardiaceae	2	e	4^{T}	Clark & Dickson 1971
Ph. clavum	Anacardiaceae	2	e	4^{T}	Clark & Dickson 1971
Tylopaedia sardonyx	Ant brood ?	?	?	$(4*)^{T}$	Clark & Dickson 1971
Trimenia wallengrenii	Ant brood ? Asteraceae (ov.)	?	?	$(4*)^{T}$	Clark & Dickson 1971
T. argyroplaga	Ant brood ?	?	?	$(4*)^{T}$	Clark & Dickson 1971
Argyrocupha malagrida	Ant brood ? Fabaceae (ov.) Asteraceae (ov.)	?	?	$(4*)^{T}$	Clark & Dickson 1971

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Aloeides thyra	Fabaceae	2	?	4(*)^T	Claassens & Dickson 1980
A. pallida	Fabaceae (lab)	2	–	(4*)^T	Clark & Dickson 1971
A. pierus	Fabaceae	2	?	3/4**	Claassens & Dickson 1980
A. depicta	Fabaceae (lab)	2	–	4**	Clark & Dickson 1971
A. gowani	Fabaceae (lab)	2	–	(4)**	Clark & Dickson 1971
A. clarki	Fabaceae (lab)	2	–	(4)**	Clark & Dickson 1971
A. aranda	Fabaceae (lab)	2	–	4**	Clark & Dickson 1971
A. henningi	Fabaceae (lab)	2	–	(4)**	Dickson 1953, Clark & Dickson 1971
A. trimeni	Sterculiaceae Fabaceae (lab)	2/4?	–	3**	Henning 1984
A. dentatis	Sterculiaceae	2	(i)	4^T	Henning 1983a
A. damarensis	Fabaceae (lab)	2?	?	(4*)^T	Clark & Dickson 1971
A. rossouwi	??	?	?	4(**)	Henning & Henning 1982
A. conradsi	??	?	?	4(**)	van Someren 1974
Erikssonia acraeina	Thymelaeaceae	1	–	4**	Henning 1984
Poecilmitis (Chrysoritis)					
zeuxo	Asteraceae	2?	–	(3)**	Clark & Dickson 1971
P. (Ch.) zonarius	Asteraceae	2?	–	(3**)	Claassens & Dickson 1980
P. (Ch.) cottrelli	Asteraceae	2?	–	(3**)	Pennington et al. 1978
P. (Poecilmitis)					
lycegenes	Anacardiaceae Ebenaceae Myrsinaceae	5	–	4**	Henning 1983a
P. lyncurium	Myrsinaceae ? Ebenaceae ?	4?	?	(4**)	Pennington et al. 1978
P. aureus	Euphorbiaceae	2?	?	4**	Henning 1983a
P. natalensis	Crassulaceae Asteraceae (lab?)	4	?	(4**)	Migdoll 1988
P. chrysaor	Crassulaceae Zygophyllaceae (lab) Anacardiaceae ?	5	–	4**	Dickson 1943
P. lycia	Crassulaceae	2?	–	(4**)	Pennington et al. 1978
P. felthami	Zygophyllaceae	2	–	4**	Clark & Dickson 1971
P. aridus	Asteraceae Zygophyllaceae (lab)	4	–	(4)**	Clark & Dickson 1971
P. pyroeis	Zygophyllaceae	2	–	4**	Clark & Dickson 1971
P. palmus	Bruniaceae Fabaceae Asteraceae Rubiaceae ?	5	–	3/4**	Clark & Dickson 1971
P. turneri	Zygophyllaceae (lab)	2?	?	(4**)	Dickson 1953
P. thysbe	Fabaceae Zygophyllaceae Asteraceae (lab)	5	y, i	4**	Clark & Dickson 1971
P. bamptoni	Zygophyllaceae Fabaceae Asteraceae	5	–	(4**)	Pennington et al. 1978
P. brooksi	Fabaceae	2?	?	4**	Henning 1987a

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Poecilmitis pan	Asteraceae	2?	?	(4**)	Pennington et al. 1978
P. trimeni	Zygophyllaceae	2?	?	(4**)	Pennington et al. 1978
P. perseus	Zygophyllaceae	2?	?	4(**)	Pennington et al. 1978, Ackery & Rajan 1990
P. braueri	Zygophyllaceae	2	?	(4*)[T]	Clark & Dickson 1971
P. atlantica	Zygophyllaceae	2?	?	(4**)	Pennington et al. 1978
P. lysander	Zygophyllaceae Fabaceae (lab)	3?	–	(4)**	Clark & Dickson 1971
P. nigricans	Asteraceae Zygophyllaceae (lab)	4	y	4**	Clark & Dickson 1971
P. uramus	Fabaceae (lab) Zygophyllaceae (lab)	4	–	(4)**	Clark & Dickson 1971
P. adonis	Zygophyllaceae (lab)	3?	–	4**	Clark & Dickson 1971
P. kaplani	Asteraceae	1?	?	(4**)	Henning 1979
Oxychaeta dicksoni	*Crematogaster* brood	?	–	4(*)[T]	Clark & Dickson 1971
Lycaenini:					
Lycaena phlaeas	Polygonaceae	3	–	0	Ballmer & Pratt 1988, 1989
L. cupreus	Polygonaceae	2	–	0	Ballmer & Pratt 1988
L. nivalis	Polygonaceae	2	–	0	Ballmer & Pratt 1988
L. helloides	Polygonaceae Rosaceae	4	–	0	Ballmer & Pratt 1988
L. dorcas	Rosaceae Ericaceae ?	2/4?	–	0	Scott 1986
L. epixanthe	Ericaceae	1	y	0	Wright 1983
L. mariposa	Ericaceae	2	–	0	Ballmer & Pratt 1988
L. heteronea	Polygonaceae	2	y	2	Ballmer & Pratt 1988
L. gorgon	Polygonaceae	2	–	0	Ballmer & Pratt 1988
L. rubidus	Polygonaceae	2	–	2	Ballmer & Pratt 1988
L. xanthoides	Polygonaceae	2	–	2	Ballmer & Pratt 1988
L. editha	Polygonaceae	2	–	2	Ballmer & Pratt 1988
L. panava	Polygonaceae	2	–	(0)	Shields 1984
L. clarki	Polygonaceae	3	–	0	Clark & Dickson 1971
L. orus	Polygonaceae	2	–	0	Clark & Dickson 1971
L. dispar	Polygonaceae	2	–	0/1?	Hinton 1951, Duffy 1968
L. hyllus	Polygonaceae	3	–	0	Klassen et al. 1989
L. virgaureae	Polygonaceae	2	–	0	SBN 1987
L. ottomanus	Polygonaceae	2	–	0	Elfferich, pers. comm.
L. thersamon	Polygonaceae Fabaceae ??	3	–	0	Larsen & Nakamura 1983, Parker 1983, Schurian et al. 1991
L. phoebus	Polygonaceae Chenopodiaceae ?	3/4?	–	0	Devarenne 1990, Rojo de la Paz & Schurian, pers. comm.
L. asabinus	Polygonaceae ?	1?	–	(0)	Schurian & Hofmann 1982
L. tityrus	Polygonaceae	2	–	0	SBN 1987
L. alciphron	Polygonaceae	2	–	0	SBN 1987
L. hippothoe	Polygonaceae	2	–	0	SBN 1987
L. candens	Polygonaceae	2	–	(0)	Higgins & Riley 1978

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Lycaena hermes	Rhamnaceae	1	y	0	Ballmer & Pratt 1988
L. arota	Grossulariaceae	2	–	0	Ballmer & Pratt 1988
L. helle	Polygonaceae	1	–	0	SBN 1987
L. salustius	Polygonaceae	2	–	0	Laidlaw 1970, Gibbs 1980
L. feredayi	Polygonaceae	2	–	0	Laidlaw 1970, Gibbs 1980
L. rauparaha	Polygonaceae	2	–	0	Gibbs 1980
L. boldenarum	Polygonaceae	2	–	0	Laidlaw 1970
Heliophorus epicles	Polygonaceae	2	–	0	Johnston & Johnston 1980, Ballmer & Pratt 1988
H. brahma	Polygonaceae	2	–	0	Sevastopulo 1973
H. sena	Polygonaceae	2	–	0	Sevastopulo 1973
Melanolycaena altimontana	Polygonaceae	2	–	0	Sibatani 1974
M. thecloides	Polygonaceae	2	–	0	Sibatani 1974

Theclini:
Luciiti
Lucia section

Lucia limbaria	Oxalidaceae	2	–	3/4(**)	Common & Waterhouse 1981
Paralucia aurifera	Pittosporaceae	3	–	4**	Common & Waterhouse 1981
P. spinifera	Pittosporaceae	2	y	4**	Edwards & Common 1978
P. pyrodiscus	Pittosporaceae	1	–	4**	Common & Waterhouse 1981, Braby 1990
Pseudodipsas eone	Verbenaceae Sapindaceae Dioscoreaceae	5	y	3(**)	Valentine & Johnson 1988
Ps. cephenes	Verbenaceae Sapindaceae Ebenaceae Loranthaceae (lab) Dioscoreaceae (lab?)	5	y	3(**)	Valentine & Johnson 1988
Acrodipsas cuprea	*Crematogaster* brood	–	–	4(*)	Common & Waterhouse 1981
A. myrmecophila	*Iridomyrmex* brood	–	–	4*	Common & Waterhouse 1981
A. illidgei	*Crematogaster* brood	–	–	4*	Samson 1989

Hypochrysops section

Hypochrysops apollo	Rubiaceae	2	e	4(**)	Common & Waterhouse 1981
H. arronica	Rubiaceae	2?	(e)	4(**)	Sands 1986
H. plotinus	Araliaceae	3	?	4(**)	Sands 1986
H. narcissus	Myrtaceae Rhizophoraceae Combretaceae Loranthaceae Myrsinaceae	5	–	3(**)	Sands 1986, Valentine & Johnson 1988
H. architas	Combretaceae	2	y	3(**)	Sands 1986
H. halyaetus	Mimosaceae Fabaceae	3	?	3(**)	Common & Waterhouse 1981
H. cyane	Myrtaceae	1?	?	3/4(**)	Common & Waterhouse 1981
H. epicurus	Verbenaceae	1?	–	3/4(**)	Common & Waterhouse 1981

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Hypochrysops delicia	Mimosaceae Rhamnaceae	4	?	3/4(**)	Common & Waterhouse 1981
H. ignitus	Mimosaceae Fabaceae Caesalpiniaceae Rosaceae Proteaceae, Myrtaceae, Lecythidaceae, Sapindaceae, Rhamnaceae, Santalaceae, Theaceae, Elaeocarpaceae, Epacridaceae, Asteraceae (total 17 families)	5	?	4**	Common & Waterhouse 1981
H. piceatus	Casuarinaceae	1?	?	3(**)	Common & Waterhouse 1981
H. miskini	Myrtaceae Melastomataceae Sapindaceae Euphorbiaceae Myrsinaceae, Verbenaceae, Dioscoreaceae, Smilacaceae	5	?	4(**)	Common & Waterhouse 1981, Sands 1986, Valentine & Johnson 1989
H. digglesii	Loranthaceae	3	–	3(**)	Common & Waterhouse 1981, Sands 1986
H. apelles	Fabaceae Mimosaceae Myrtaceae Barringtoniaceae, Lecythidaceae, Rhizophoraceae, Combretaceae, Rhamnaceae, Euphorbiaceae, Verbenaceae	5	?	4**	Common & Waterhouse 1981, Sands 1986, Ballmer & Pratt 1988
H. dicomas	??	?	?	4(**)	Sands 1986
H. byzos	Rhamnaceae	2	?	1/2(**)	Common & Waterhouse 1981
H. geminatus	Sterculiaceae	2	?	(1/2**)	Sands 1986
H. pythias	Sterculiaceae Tiliaceae ??	3?	?	0(?**)	Valentine & Johnson 1988
H. polycletus	Malpighiaceae (ov.)	?	?	4?(**)	Sands 1986
H. theon	Polypodiaceae	1?	e	3/4(**)	Common & Waterhouse 1981
H. dohertyi	Polypodiaceae (ov.)	1?	?	(3**)	Sands 1986
Philiris nitens	Euphorbiaceae	1?	(–)	0	Common & Waterhouse 1981, Ballmer & Pratt 1988
Ph. helena	Euphorbiaceae	2	–	0/1	Parsons 1984
Ph. agatha	Euphorbiaceae	2	–	0/1	Parsons 1984
Ph. innotata	Moraceae	2?	(–)	(0)	Common & Waterhouse 1981
Ph. moira	Moraceae	2	–	0*?	Forbes 1977
Ph. kapaura	Moraceae ?	(2)	(–)	(0)	Parsons 1984
Ph. ziska	Moraceae	1	–	2/3**?	Parsons 1984
Ph. intensa	Urticaceae	1?	–	2*?	Parsons 1984
Ph. fulgens	Lauraceae	2?	–	0	Wood 1984
Ph. diana	Lauraceae	2?	–	0	Wood 1984
Ph. harterti	Lauraceae	2?	–	(0)	Parsons 1984
Ph. violetta	Lauraceae	2?	–	(0)	Parsons 1984
Ph. praeclara	Lauraceae	2?	–	(0)	Parsons 1984
Ogyriti					
Ogyris genoveva	Loranthaceae	3	–	4**	Common & Waterhouse 1981
O. zosine	Loranthaceae	2	–	3**	Common & Waterhouse 1981
O. idmo	Loranthaceae ?	?	?	(3/4**)	Common & Waterhouse 1981

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Ogyris otanes	Santalaceae	2?	–	4**	Common & Waterhouse 1981
O. abrota	Loranthaceae	3	–	3**	Common & Waterhouse 1981
O. olane	Loranthaceae	3	–	2**	Common & Waterhouse 1981
O. barnardi	Loranthaceae	2?	–	3**	Common & Waterhouse 1981
O. ianthis	Loranthaceae	3	–	3**	Common & Waterhouse 1981
O. iphis	Loranthaceae	3	–	3**	Common & Waterhouse 1981
O. aenone	Loranthaceae	3	–	3**	Common & Waterhouse 1981
O. oroetes	Loranthaceae	2?	–	(3**)	Common & Waterhouse 1981
O. amaryllis	Loranthaceae	2	–	3/4**	Common & Waterhouse 1981

Zesiiti
Zesius chrysomallus	Fabaceae	5	y	4*(*)	Bell 1915, Yates 1932,
	Mimosaceae ?				Hinton 1951
	Combretaceae				
	Anacardiaceae				
	Dioscoreaceae				
	+ *Zesius* larvae/pupae, + *Oecophylla* brood ?				
Jalmenus evagoras	Mimosaceae	2	y	4**	Common & Waterhouse 1981
J. eichhorni	Mimosaceae	2	(y)	3**	Common & Waterhouse 1981
J. ictinus	Mimosaceae	4	(y)	4**	Common & Waterhouse 1981
	Sapindaceae				
J. pseudictinus	Mimosaceae	4	(y)	4**	Common & Waterhouse 1981
	Sapindaceae				
J. daemeli	Mimosaceae	5	y	4**	Common & Waterhouse 1981
	Myrtaceae				
	Sapindaceae				
J. lithochroa	Mimosaceae	1?	y, i	3**	Common & Waterhouse 1981
J. inous	Mimosaceae	1?	(y)	3**	Common & Waterhouse 1981
J. icilius	Mimosaceae	3	(y)	3/4**	Common & Waterhouse 1981
	Caesalpiniaceae				
J. clementi	Mimosaceae	2	(y)	2/3**	Common & Waterhouse 1981
Pseudalmenus					
chlorinda	Mimosaceae	2	y	3/4**	Common & Waterhouse 1981

Arhopaliti
Arhopala
amphimuta	Euphorbiaceae	1?	y	3/4**	Maschwitz et al. 1984
A. moolaiana	Euphorbiaceae	1?	y	3/4**	Maschwitz et al. 1984
A. zylda	Euphorbiaceae	1?	y	3/4**	Maschwitz et al. 1984
A. bazalus	Fagaceae	3	?	3**	Iwase 1954
A. amantes	Fabaceae ?	4?	?	3**	Viehmeyer 1910b,
	Combretaceae ?				Bell 1915
A. pseudocentaurus	Fagaceae	5	y	4**	Norman 1949,
	Lythraceae				Corbet & Pendlebury 1978,
	Myrtaceae				Kirton & Kirton 1987,
	Combretaceae				Ballmer & Pratt 1988

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Arhopala centaurus	Myrtaceae Combretaceae Lythraceae Loranthaceae	5	y	4**	Valentine & Johnson 1988
A. micale	Lauraceae Lythraceae Myrtaceae Combretaceae Sapindaceae Euphorbiaceae	5	(y)	3**	Common & Waterhouse 1981
A. madytus	Combretaceae Sterculiaceae Malvaceae Boraginaceae Verbenaceae	5	(y)	(3**)	Valentine & Johnson 1988
A. meander	??	?	?	(3**)	Viehmeyer 1910a
A. japonica	Fagaceae	3	?	3*(*)	Iwase 1954
A. rama	Fagaceae	2?	?	(3**)	Sevastopulo 1973
A. ganesa	Fagaceae	3	?	3**	Iwase 1954
A. birmana	Fagaceae	3?	?	(3**)	Uchida 1984
A. (Mahathala) ameria	Euphorbiaceae Boraginaceae	4	?	(3)**	Uchida 1984
Thaduka multicaudata	Euphorbiaceae	1?	y	2/3**	Bell 1915, Hinton 1951
Flos apidanus	Myrtaceae Lythraceae	4	?	(3**)	Corbet & Pendlebury 1978
F. areste	??	?	?	(3)**	Ballmer & Pratt 1988
F. fulgida	??	?	?	3**	Ballmer & Pratt in press
Surendra quercetorum	Mimosaceae	3	y	3**	Bell 1915
ssp.? *vivarna*	Mimosaceae	1?	y	3**	Maschwitz et al. 1985b
Thecliti					
Artopoetes pryeri	Oleaceae	3	y, i	(0)	Shirôzu 1961 [62], Shirôzu & Hara 1974
Coreana raphaelis	Oleaceae	2	y, i	(0)	Iwase 1954
Ussuriana michaelis	Oleaceae	2	?	(0)*?	Shin 1970
U. ibara	Oleaceae	2	?	(0*)	Iwase 1954
U. stygiana	Oleaceae	2	?	0(*)	Shirôzu 1961 [62]
Laeosopis roboris	Oleaceae	2	–	(0)*?	Agenjo 1963
Thecla betulae	Rosaceae Betulaceae (lab ?) Corylaceae (lab ?) Salicaceae ??	4/5?	y	1 pupa: 3	Shirôzu 1961 [62], Emmet & Heath 1990
Th. betulina	Rosaceae	· 2	(y)	(0/1)	Shirôzu 1961 [62]
Shirozua jonasi	Fagaceae Anacardiaceae ? Lachnidae Coccidae + *Lasius* regurgitations	2/4?	?	4	Shirôzu 1961 [62], Cottrell 1984, Pierce & Elgar 1985

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Antigius attilia	Fagaceae	3	?	(0)	Shirôzu 1961 [62]
A. butleri	Fagaceae	2/3	?	0(*?)	Shirôzu 1961 [62]
Wagimo signata	Fagaceae	2/3	?	(0)	Iwase 1954,
+ ssp. *quercivora*	Fagaceae	2	?	(0)	Shirôzu 1961 [62]
Araragi enthea	Juglandaceae	3/4	y	(0*?)	Iwase 1954,
	Fagaceae (lab?)				Shirôzu 1961 [62]
Chaetoprocta odata	Juglandaceae	2	?	(0)	Sevastopulo 1973
Japonica lutea	Fagaceae	3	?	(0)	Shirôzu 1961 [62]
J. saepestriata	Fagaceae	3	?	(0)	Iwase 1954
Habrodais grunus	Fagaceae	3	y	0	Ballmer & Pratt 1988
Iratsume orsedice	Hamamelidaceae	2	?	(0)	Iwase 1954
Neozephyrus taxila	Betulaceae	2/5	?	(0)	Iwase 1954,
	Fagaceae (lab?)				Shirôzu 1961 [62]
	Rosaceae (?, lab?)				
Chrysozephyrus					
birupa	Ericaceae	2?	?	(0)	Sevastopulo 1973
Ch. smaragdinus	Rosaceae	5	?	(0)	Shirôzu 1961 [62]
	Fagaceae				
	Corylaceae				
	Ulmaceae (lab?)				
Ch. aurorinus	Fagaceae	2/3	?	(0)	Shirôzu 1961 [62]
Ch. hisamatsusanus	Fagaceae ?	2	?	(0)	Iwase 1954
Ch. ataxus	Fagaceae	2/3	?	(0)	Shirôzu 1961 [62]
Hypaurotis crysalus	Fagaceae	1?	?	0	Scott 1986
Favonius orientalis	Fagaceae	2/3	(i)	(0)	Shirôzu 1961 [62]
F. yuasai	Fagaceae	2	y, i	(0)	Iwase 1954
F. ultramarinus	Fagaceae	2/3	i	(0)	Shirôzu 1961 [62]
ssp. *jezoensis*	Fagaceae	2/3	i	(0)	Iwase 1954
ssp. *hayashii*	Fagaceae	2	(i)	(0)	Iwase 1954
F. saphirinus	Fagaceae	2/3	(i)	(0)	Shirôzu 1961 [62]
F. cognatus	Fagaceae	2/3	i	(0)	Shirôzu & Hara 1974
F. latifasciatus	Fagaceae	2/3	y	(0)	Shirôzu 1961 [62]
F. fujisanus	Fagaceae	2/3	(i)	(0)	Shirôzu 1961 [62]
Quercusia quercus	Fagaceae	2/5?	y, i	0	Shirôzu 1961 [62],
	Myricaceae (lab ?)			pupa: 2	Emmet & Heath 1990
	Oleaceae (lab ?)				
Amblopala avidiena	Mimosaceae	2?	y	(3)**	Uchida 1985
Eumaeini:					
Catapaecilmatiti					
Catapaecilma major	Combretaceae	2?	(y)	3(**)	Corbet & Pendlebury 1978
C. elegans	Combretaceae	2	y	3**	Hinton 1951
Amblypodiiti					
Amblypodia anita	Olacaceae	2?	y	0**	Bell 1915, Hinton 1951
Iraota rochana	Moraceae	2	(y)	(2**)	Corbet & Pendlebury 1978

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Iraota timoleon	Moraceae	2	y, f, e	2**	Bell 1915, Corbet & Pendlebury 1978
Myrina silenus	Moraceae	2	y, f, e	3**	Henning 1983a
M. dermaptera	Moraceae	2	–	2**	Clark & Dickson 1971
M. subornata	Moraceae	2	–	(2)**	Hinton 1951
M. sharpei	Moraceae (ov.)	2	?	(2**)	van Someren 1974
M. annettae	Moraceae	2	?	(2**)	Ackery & Rajan 1990
Loxuriti					
Loxura atymnus	Dioscoreaceae Smilacaceae	3	y	3**	Corbet & Pendlebury 1978, pers. obs.
L. cassiopeia	Dioscoreaceae	2	y	(3**)	Pinratana 1981
Yasoda pita	Dioscoreaceae Smilacaceae	3	(y)	(3**)	Corbet & Pendlebury 1978
Eooxylides tharis	Dioscoreaceae Smilacaceae	3	y	3**	Corbet & Pendlebury 1978,
Cheritra freja	Mimosaceae Lauraceae Rubiaceae	5	y	0	Bell 1915, Corbet & Pendlebury 1978, Ballmer & Pratt 1988
Drupadia ravindra	Mimosaceae Caesalpiniaceae Myrtaceae	5	y	3**	Corbet & Pendlebury 1978, pers. obs.
D. theda	Caesalpiniaceae Rubiaceae	4	y, i	3**	Maschwitz et al. 1985b, pers. obs.
Dapidodigma demeter	Mimosaceae	2?	?	?	Ackery & Rajan 1990
Horaga albimacula anyta	Euphorbiaceae	2?	?	?	Uchida 1984
H. onyx	Coriariaceae	1?	?	?	Sevastopulo 1973
Rathinda amor	Myrtaceae Sapindaceae Euphorbiaceae Loranthaceae Styracaceae Rubiaceae	5	i, f	?	Bell 1915, Sevastopulo 1938, 1973
Iolaiti					
Iolaus (Iolaus) bolissus	Loranthaceae	2	?	?	Kielland 1990
I. (Hemiolaus) coeculus	Olacaceae	1?	?	?	Migdoll 1988
I. (Stugeta) bowkeri	Loranthaceae Olacaceae	4	–	0?**	Clark & Dickson 1971, Kielland 1990
I. (S.) marmorea	Olacaceae	2	y	0?	Jackson 1937
I. (S.) mimetica	Olacaceae Loranthaceae (ov)	4	?	?	van Someren 1974, Sevastopulo 1975
I. (S.) carpenteri	Olacaceae Loranthaceae (ov)	4	y, i	?	van Someren 1974, Sevastopulo 1975

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Iolaus (Pseudiolaus)					
poultoni	Loranthaceae	3	y, i	?	van Someren 1974, Kielland 1990
I. (Tanuetheira)					
timon	Loranthaceae	1?	i	0?	Farquharson 1922
I. (Argiolaus) silas	Loranthaceae	3	(y)	0?**	Clark & Dickson 1971
I. (A.) silarus	Loranthaceae	3	(y)	(0?**)	Henning & Henning 1984, Kielland 1990
I. (A.) crawshayi	Loranthaceae	3	y, i	0?	Jackson 1937, Kielland 1990
I. (A.) lalos	Loranthaceae	2?	?	?	Kielland 1990
I. (A.) stewarti	Loranthaceae	2	?	?	Ackery & Rajan 1990
I. (Iolaphilus)					
alcibiades	Loranthaceae	2	i	2?(*?)	Farquharson 1922
I. (I.) julus	Loranthaceae	2	i	2*	Farquharson 1922, Hinton 1951
I. (I.) menas	Loranthaceae	2	?	?	Ackery & Rajan 1990
I. (I.) paneperata	Loranthaceae	2	i	0*	Farquharson 1922
I. (I.) trimeni	Loranthaceae	3	–	(0?)**	Henning 1983a
I. (I.) ismenias	Loranthaceae	2	?	?	Ackery & Rajan 1990
I. (I.) iturensis	Loranthaceae	2	?	?	Kielland 1990
I. (I.) maritimus	Loranthaceae	3	?	?	Kielland 1990
I. (I.) ndolae	Loranthaceae	3	?	?	Kielland 1990
I. (I.) cottrelli	Loranthaceae (ov.)	2	?	?	Kielland 1990
I. (I.) poecilaon	Loranthaceae	2	?	?	Ackery & Rajan 1990
I. (Philiolaus)					
parasilanus	Loranthaceae	2	?	?	van Someren 1974
I. (Ph.) dianae	Loranthaceae	2	?	?	Ackery & Rajan 1990
I. (Aphniolaus)					
pallene	Olacaceae Loranthaceae	4	–	?	Sevastopulo 1975, Kielland 1990
I. (Epamera) sidus	Loranthaceae	3	y, i	0?**	Clark & Dickson 1971, Kielland 1990
I. (E.) mimosae	Loranthaceae	3	–	0?**	Clark & Dickson 1971, Kielland 1990
I. (E.) laon	Loranthaceae	1?	i	0?	Farquharson 1922
I. (E.) farquharsoni	Loranthaceae	1?	i	0?	Farquharson 1922
I. (E.) tajoraca	Loranthaceae	1?	y, i	0?	Jackson 1937, van Someren 1974
I. (E.) aphnaeoides	Loranthaceae	3	?	?	Kielland 1990
+ ssp. *diametra*	Loranthaceae	2?	i	?	Kielland 1990
+ ssp. *nasisii*	Loranthaceae	3	y, i	?	Kielland 1990
I. (E.) australis	Loranthaceae	2?	?	?	Kielland 1990
I. (E.) congdoni	Loranthaceae	2	?	?	Kielland 1990
I. (E.) mursei	Loranthaceae	2	?	?	Ackery & Rajan 1990
I. (E.) penningtoni	Loranthaceae	2	?	?	Ackery & Rajan 1990
I. (E.) scintillans	Loranthaceae	2	?	?	Ackery & Rajan 1990
I. (E.) dubiosa	Loranthaceae	3	?	?	Kielland 1990
I. (E.) pseudopollux	Loranthaceae	2?	?	?	Kielland 1990
I. (E.) arborifera	Loranthaceae (ov)	2?	?	?	van Someren 1974
I. (E.) helenae	Loranthaceae	1?	?	?**	Henning & Henning 1989

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Iolaus (Epamera) *iasis*	Loranthaceae	1?	i	0?	Farquharson 1922, van Someren 1974
I. (E.) mermis	Loranthaceae	2?	?	?	Kielland 1990
I. (E.) violacea	Loranthaceae	2?	?	?	Kielland 1990
I. (E.) aethria	Loranthaceae	2	(i)	0?	Farquharson 1922
I. (E.) bansana	Loranthaceae	1?	y, i	?	Jackson 1937, van Someren 1974
I. (E.) glaucus	Loranthaceae	2/3	i	2(**)	Larsen 1980, Ackery & Rajan 1990
I. (E.) alienus	Loranthaceae	3	–	0?**	Clark & Dickson 1971, Kielland 1990
I. (E.) aemulus	Loranthaceae	2	i	?**	Migdoll 1988
I. (E.) obscurus	Loranthaceae	2	(i)	?	Pennington et al. 1978
I. (E.) maesa	Loranthaceae	2	i	3(**)	Farquharson 1922
Pratapa deva	Loranthaceae	2	?	2**	Corbet & Pendlebury 1978
Creon cleobis	Loranthaceae	3	y	2**	Bell 1915, Hinton 1951, Johnston & Johnston 1980
Tajuria cippus	Loranthaceae	3	?	1/2**	Bell 1915, Corbet & Pendlebury 1978
T. melastigma	Loranthaceae	2	?	(2**)	Sevastopulo 1973
T. diaeus	Loranthaceae Verbenaceae ??	2	?	(2**)	Sevastopulo 1973
T. mantra	Loranthaceae	2?	?	(2**)	Corbet & Pendlebury 1978
T. deudorix	Loranthaceae	2	?	(2**)	Corbet & Pendlebury 1978
T. dominus	Loranthaceae	2?	?	(2**)	Corbet & Pendlebury 1978
T. caerulea	Loranthaceae	2?	?	(2**)	Uchida 1985
Charana mandarinus	Loranthaceae ?	2?	?	(1**)	Toxopeus 1933
Eliotia jalindra	Loranthaceae	2	?	(1**)	Sevastopulo 1973
+ ssp. *indra*	Loranthaceae	2	?	1**	Bell 1915, Hinton 1951
Jacoona anasuja	Loranthaceae	2?	?	(2**)	Corbet & Pendlebury 1978
Remelaniti					
Ancema blanka	Loranthaceae	2	?	(2)*	Bell 1915, Hinton 1951
Remelana jangala	Hypericaceae Myrsinaceae Ericaceae	5	?	3*	Johnston & Johnston 1980, Young 1991
Hypolycaeniti					
Hypolycaena erylus	Rubiaceae Lauraceae	4	(y)	4*	Jacobson 1912, Corbet & Pendlebury 1978
H. phorbas	Caesalpiniaceae Myrtaceae Lecythidaceae Rhizophoraceae Combretaceae, Sapindaceae, Loranthaceae, Myrsinaceae, Verbenaceae, Flagellariaceae	5	y, i	4*	Common & Waterhouse 1981, Valentine & Johnson 1988, Moss 1989
H. pachalica	Combretaceae (ov) Cucurbitaceae	4	(i, f)	(3*)	van Someren 1974, Kielland 1990

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Hypolyc. philippus	Sapindaceae Punicaceae Olacaceae Loranthaceae	5	i, f, e	3*	Clark & Dickson 1971, Sevastopulo 1975, Ackery & Rajan 1990
	Cucurbitaceae, Rubiaceae, Bignoniaceae, Verbenaceae, Fabaceae ?				
H. nigra	??	?	?	3(*)	Hinton 1951
H. danis	Orchidaceae	3	y, i, f	(2*)	Common & Waterhouse 1981
H. (Tatura) lebona	??	?	?	3*(*)	Hinton 1951
H. (Chliaria) kina	Orchidaceae	3	i	(2*)	Corbet & Pendlebury 1978
H. (Ch.) othona	Orchidaceae	3	i, f, e	2**(?)	Bell 1915, Hinton 1951
Leptomyrina hirundo	Crassulaceae	3	e	3*	Migdoll 1988
L. lara	Crassulaceae Aizoaceae	4	e	2/3*	Sevastopulo 1975, Migdoll 1988
L. henningi	Crassulaceae	3	(e)	(2*)	Pennington et al. 1978
L. gorgias	Crassulaceae Aizoaceae	4	e ·	2/3*	Migdoll 1988, Kielland 1990

Deudorigiti
Deudorix (Virachola)

diocles	Caesalpiniaceae Mimosaceae Fabaceae Rosaceae	5	i, f, e	2/3*	Migdoll 1988
	Proteaceae, Myrtaceae, Combretaceae				
D. lorisona	Rubiaceae	2?	f, e	?(*)	Kielland 1990
D. vansomereni	Connaraceae	1?	f, e	?(*)	van Someren 1974
D. dariaves	Sapindaceae Caesalpiniaceae Rubiaceae	5	i, f, e	?(*)	Sevastopulo 1975, Migdoll 1988
D. dinomenes	Sapindaceae	1?	f, e	?(*)	Sevastopulo 1975
D. odana	Fabaceae Caesalpiniaceae	3	i, f, e	?(*)	Jackson 1947, Sevastopulo 1975
D. dinochares	Mimosaceae Fabaceae Rosaceae Proteaceae	5	i, f, e	2/3*(*?)	Clark & Dickson 1971
	Myrtaceae, Combretaceae, Olacaceae, Rubiaceae				
D. antalus	Mimosaceae Fabaceae Caesalpiniaceae Rosaceae	5	i, f, e	3*(*?)	Jackson 1937, Clark & Dickson 1971, Sevastopulo 1975, Ackery & Rajan 1990
	Myrtaceae, Combretaceae, Sapindaceae, Olacaceae, Apiaceae, Solanaceae, Aitoniaceae etc.				
D. ecaudata	Mimosaceae	2?	e (galls)	3(*)	van Someren 1974
D. suk	Mimosaceae	2?	e (galls)	3(*)	van Someren 1974
D. vansoni	Mimosaceae	2?	e (galls)	(3*)	Pennington et al. 1978
D. penningtoni	Mimosaceae	2?	e (galls)	(3*)	Kielland 1990

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Deudorix isocrates	Fabaceae Rosaceae Lythraceae Myrtaceae Punicaceae, Rubiaceae, Loganiaceae	5	i, f, e	1(*)[T]	Bell 1920, Hinton 1951
D. perse	Punicaceae Myrtaceae Rubiaceae	5	i, f, e	1[T]	Bell 1920, Hinton 1951
D. livia	Fabaceae Mimosaceae Caesalpiniaceae Rosaceae Punicaceae, Myrtaceae, Solanaceae, Alliaceae, Arecaceae	5	i, f, e	2/3*	Hinton 1951, Awadallah et al. 1971, Larsen 1980
D. democles	Loganiaceae	2?	f, e	?	Common & Waterhouse 1981
D. smilis	Loganiaceae	2?	f, e	?	Common & Waterhouse 1981
D. jacksoni	Loranthaceae	1?	y	(0)**(?)	Jackson 1937
D. (Pilodeudorix) diyllus	Fabaceae	1?	i, f	3*(*?)	Farquharson 1922
D. camerona	Fabaceae	1?	i, f	2**	Jackson 1947
D. (Hypokopelates) obscura	??	?	?	3(*?)	Hinton 1951
D. (Deudorix) epijarbas	Punicaceae Proteaceae Sapindaceae Hippocastanaceae Connaraceae, Arecaceae, Rosaceae (lab)	5	i, f, e	?*	Hinton 1951, Common & Waterhouse 1981, Ballmer & Pratt 1988
D. epirus	Sapindaceae	2?	f, e	?	Common & Waterhouse 1981
Artipe eryx	Rubiaceae	1?	i, f, e	0	Shirôzu & Hara 1974, Johnston & Johnston 1980
Sinthusa chandrana	Rosaceae	2?	y, (e?)	?	Johnston & Johnston 1980
Bindahara phocides	Hippocrateaceae	5	f, e	0	Storey & Lambkin 1983
+ ssp. *sugriva*	Rhamnaceae Celastraceae		i, f, e	0/1*	Bell 1915, Hinton 1951
Rapala pheretima	Caesalpiniaceae Lythraceae	4	y, i	3(**)	Norman 1976
R. dieneces	Myrtaceae	3	(i, f)	(2**)	Corbet & Pendlebury 1978
R. iarbus	Fabaceae Melastomataceae Sapindaceae Rhamnaceae	5	y, i	3**	Sevastopulo 1973, Corbet & Pendlebury 1978, pers. obs.
R. manea	Mimosaceae Caesalpiniaceae Fabaceae Rosaceae Sapindaceae, Combretaceae, Theaceae, Caprifoliaceae, Verbenaceae	5	i, f	3**	Hinton 1951, Sevastopulo 1973, Seki et al. 1991
R. nissa rectivitta	??	?	?	(2)**	Sevastopulo 1941

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Rapala varuna	Fabaceae Mimosaceae Myrtaceae Sapindaceae Rhamnaceae Verbenaceae	5	y, i, f, e	(1/2**)	Jayaraj et al. 1961, Common & Waterhouse 1981, Lambkin 1983, Valentine & Johnson 1988
R. rhoecus (?) [as *sphinx*]	Melastomataceae Elaeagnaceae	4	(y, i)	(2**)	Sevastopulo 1973
R. selira	Fabaceae	2?	(y, i)	(2**)	Sevastopulo 1973
R. arata	Fabaceae Saxifragaceae Rosaceae Ericaceae Symplocaceae Rhamnaceae	5	i, f	3**	Iwase 1954, Shirôzu & Hara 1974
R. caerulea	Fabaceae	3?	(i?)	(2**)	Uchida 1985
R. takasagonis	Piperaceae	2?	(i?)	(2**)	Uchida 1985
Capys alphaeus	Proteaceae	2	i, f, e	(0)*	Clark & Dickson 1971
ssp.? *brunneus*	Proteaceae	2	i, e	(0*)	Kielland 1990
C. penningtoni	Proteaceae	2	i, f	(0*)	Migdoll 1988
C. disjunctus	Proteaceae	2	i, f, e	(0)*	Clark & Dickson 1971
ssp.? *connexivus*	Proteaceae	2	i, e	(0*)	Kielland 1990
C. catharus	Proteaceae	2	i, e	(0)*	Jackson 1947
Tomares ballus	Fabaceae	3	(i, f)	2**	Martín 1982, Jordano et al. 1990a & b
T. romanovi	Fabaceae	2?	i, f	3(**)	Weidenhoffer & Vanek 1977
T. callimachus	Fabaceae	1?	(i, f)	3**	Malicky 1969b, Weidenhoffer & Vanek 1977
T. nogelii	Fabaceae	2	i, f	3(**)	Hesselbarth & Schurian 1985
T. nesimachus	Fabaceae	1	(i)	(3**)	Larsen & Nakamura 1983
T. mauritanicus	Fabaceae	1?	y, i	(3)**	Malicky 1969b, Courtney 1983
Eumaeiti:					
Eumaeus atala	Cycadaceae Euphorbiaceae ?	3/4?	y	0	Ehrlich & Raven 1964, Scott 1986
Eu. minijas	Cycadaceae	3	y	0	Scott 1986
Eu. childrenae	Cycadaceae Amaryllidaceae ? Agavaceae ?	3/4?	y	0	Ross 1964b, Ehrlich & Raven 1964
Eu. godartii	Cycadaceae	2	(y)	0	DeVries, pers. comm.
Eu. toxea [as *minyas*]	Cycadaceae	3	y	0	Ross 1964b
Micandra platypera	Fabaceae	2	y	?	DeVries, pers. comm.
Evenus regalis	Sapotaceae	3	y, i, f	?	Zikan 1956, Kendall 1975
E. coronata	Sapotaceae	2	y	?	Schultze-Rhonhof 1938
E. latreillii	Sapotaceae	2	y	?	Hoffmann 1937b

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Allosmaitia coelebs	Malpighiaceae	2?	y, e	?	Riley 1975
Theritas triquetra	Melastomataceae Euphorbiaceae Ulmaceae	5	y	?	Jörgensen 1935, Hoffmann 1937a
Pseudolycaena damo	Fabaceae Rosaceae Sapindaceae Euphorbiaceae	5	y, i	3*	Kendall 1975, Robbins & Aiello 1982, DeVries 1990a
Ps. marsyas	Rosaceae Myrtaceae Combretaceae Anacardiaceae	5	y, i	(3*?)	Kirkpatrick 1953, Zikan 1956, d'Araujo e Silva et al. 1967/68
	Sapindaceae, Celastraceae, Sterculiaceae, Sapotaceae, Ulmaceae				
Ps. nellyae	Fabaceae Annonaceae Meliaceae Malpighiaceae Sapotaceae	5	(y)	?	Lamas 1975
Arcas ducalis	Annonaceae	2?	?	0	Zikan 1956
Atlides halesus	Loranthaceae	2	i	0*	Ballmer & Pratt 1988
A. near *cosa* [as *atys*]	Loranthaceae	1?	?	(0*)	Zikan 1956
Arawacus lincoides [as *aetolus*]	Solanaceae	3	(-)	3*	Robbins & Aiello 1982, Robbins, in press
A. separata [as *aetolus*]	Solanaceae	2?	(-)	(3*)	Robbins & Aiello 1982
A. meliboeus	Solanaceae	2	(-)	(3*)	Hoffmann 1937a
A. jada	Solanaceae	2	-	(3*)	Scott 1986
A. ellida	Solanaceae	2?	-	(3*)	Robbins 1991
Thereus pedusa	Loranthaceae	1?	y, i	3*	DeVries, pers. comm.
Th. near *enenia*	Malpighiaceae Chrysobalanaceae Malvaceae (lab)	5	y, i	3*	Robbins & Aiello 1982, DeVries 1990a
Rekoa palegon	Euphorbiaceae Ulmaceae Solanaceae Boraginaceae Verbenaceae Asteraceae	5	y, i, e	3*	Malicky 1969b, DeVries 1990a, Robbins 1991
R. marius	Fabaceae Caesalpiniaceae Polygonaceae Myrtaceae	5	y, i, f, e	0?(*)	Robbins & Aiello 1982, Robbins 1991
	Melastomataceae, Combretaceae, Sapindaceae, Malpighiaceae, Ochnaceae, Apocynaceae, Boraginaceae, Bignoniaceae, Verbenaceae				
R. stagira	Fabaceae Malpighiaceae	4	y	?	Robbins 1991
R. zebina	Fabaceae	3?	i	?	Robbins 1991
Contrafacia muattina	Fabaceae	2?	y	0	Hoffmann 1932

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Chlorostrymon					
simaethis	Sapindaceae	5	f, e	2/3(*)	Zikan 1956, Scott 1986,
	Asteraceae				DeVries 1990a & pers comm.
	Fumariaceae ?				
	Solanaceae ?				
	Scrophulariaceae ?				
Ch. maesites	Mimosaceae (lab)	3	i, f	(2*)	Scott 1986
Harkenclenus titus	Rosaceae	3/4?	y, i, f	2*	Harvey & Webb 1980,
	Fagaceae ?				Klassen et al. 1989
Satyrium (Fixsenia)					
pruni	Rosaceae	2	i	0	Kitching & Luke 1985
S. (F.) watarii	Rosaceae	2?	?	(0)	Uchida 1985
S. (F.) favonius	Fagaceae	2	y, i	(0)	Scott 1986
S. (F.) polingi	Fagaceae	2	(y, i)	(0)	Scott 1986
S. formosana	Sapindaceae	2?	?	?(*)	Uchida 1985
S. w-album	Ulmaceae	5	i, f	2*	SBN 1987
	Fagaceae				
	Rosaceae				
	Rhamnaceae				
	Tiliaceae				
S. spini	Rhamnaceae	2	–	2*	SBN 1987
S. jebelia	Rhamnaceae	1	(–)	(2*)	Larsen 1990
S. merus	Rhamnaceae	2	?	?*	Iwase 1954
S. iyonis	Rhamnaceae	2	?	?*	Taketsuka & Akizawa 1978
S. saepium	Rhamnaceae	2?	?	?*	Ballmer & Pratt 1988
S. californica	Fagaceae	5	–	?*	Ballmer & Pratt 1988
	Rosaceae				
	Rhamnaceae				
	Salicaceae				
S. acadica	Salicaceae	2	–	?*	Scott 1986
S. sylvinus	Salicaceae	2	–	?*	Ballmer & Pratt 1988
S. liparops	Rosaceae	5	y, i, f	?(*)	Scott 1986
	Fagaceae				
	Betulaceae				
	Juglandaceae				
	Salicaceae				
	Ericaceae				
	Oleaceae				
S. kingi	Symplocaceae	4	y	?(*)	Scott 1986
	Ericaceae (lab)				
S. caryaevorus	Fagaceae	5	–	?(*)	Scott 1986
	Juglandaceae				
	Oleaceae				
	Rosaceae ?				
S. calanus	Fagaceae	5	y, i	?(*)	Scott 1986
	Juglandaceae				
	Rosaceae				
	Aceraceae				
	Oleaceae				
S. auretorum	Fagaceae	2	–	?*	Ballmer & Pratt 1988
S. edwardsii	Fagaceae	2	y	3/4*	Webster & Nielsen 1984

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Satyrium ilicis	Fagaceae	2	y	2*	SBN 1987
S. esculi	Fagaceae	2	(y)	3*	Martín & Gurrea 1983, Devarenne 1990
S. myrtale	Rosaceae	2/3	?	(0*)	Nakamura 1976
S. acaciae	Rosaceae	3	i	0*	SBN 1987
+ ssp.? *persica*	Rosaceae ?	2?	?	(0)	Larsen 1974
S. marcida	Rosaceae ?	2?	?	?	van Oorschot et al. 1985
S. behrii	Rosaceae	2	–	?*	Ballmer & Pratt 1988
S. tetra	Rosaceae	2?	–	?*	Ballmer & Pratt 1988
S. ledereri	Fabaceae ?	?	?	?(*)	Olivier 1989
S. hyrcanica	Fabaceae ?	?	?	?(*)	Olivier 1989
S. rhymnus	Fabaceae	?	?	(3*)	Zhdanko 1983
S. tengstroemi	Fabaceae	2?	?	3*	Viehmeyer 1907, Eckweiler, pers. comm.
S. sinensis	Fabaceae ?	2?	?	(3*)	Eckweiler, pers. comm.
S. fuliginosum	Fabaceae	2	?	3*	Ballmer & Pratt 1988
Callophrys rubi	Fabaceae Rosaceae Rhamnaceae Cistaceae Cornaceae, Ericaceae, Caprifoliaceae, + lab: Ranunculaceae, Polygonaceae, Hippocastanaceae, Oxalidaceae, Geraniaceae, Tiliaceae, Asteraceae, Alliaceae	5	y, i, f	0/1*	SBN 1987, Fiedler 1990d
C. avis	Ericaceae	3	i, f	(0*)	Dujardin 1972, Martín 1982, Devarenne 1990
C. affinis	Polygonaceae	2/3	i, f	(0*)	Scott 1986
C. perplexa	Fabaceae Polygonaceae	4	i, f	0*	Ballmer & Pratt 1988
C. dumetorum	Polygonaceae Fabaceae	4	i, f	0*	Ballmer & Pratt 1988
C. sheridanii	Polygonaceae	2	–	(0*)	Scott 1986
C. lemberti	Polygonaceae Fabaceae	4	–	0*	Ballmer & Pratt 1988
C. comstocki	Polygonaceae	1?	–	0*	Ballmer & Pratt 1988
C. (Incisalia) eryphon	Pinaceae Cupressaceae	3	y, i. e	0*	Ballmer & Pratt 1988
C. (I.) niphon	Pinaceae Cupressaceae ?	3	y	(0*)	Scott 1986
C. (I.) lanoraieensis	Pinaceae	2	y	(0*)	Scott 1986
C. (Sandia) irus	Fabaceae	3	i, f	(0*)	Scott 1986
C. (S.) henrici	Fabaceae Rosaceae Ebenaceae Aquifoliaceae Ericaceae, Caprifoliaceae, Cyrillaceae ?	5	y, i, f, e	(0*)	Scott 1986
C. (S.) polios	Ericaceae	3	y, i	(0*)	Scott 1986

Table **17** *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Callophrys (Sandia) augustinus	Rosaceae Polygonaceae Rhamnaceae Ericaceae Hydrophyllaceae, Convolvulaceae, Liliaceae	5	i, f, e	0*	Ballmer & Pratt 1988, Klassen et al. 1989
C. (S.) fotis	Rosaceae	1?	i, f	0*	Ballmer & Pratt 1988
C. (S.) mossii	Crassulaceae	2	i, e	0*	Emmel & Ferris 1972
C. (S.) xami	Crassulaceae	3	e	2(*)	Ziegler & Escalante 1964, Scott 1986
C. (S.) mcfarlandi	Agavaceae	2	i, f	2*	Scott 1986
C. (Mitoura) nelsoni	Cupressaceae	2	y	0*	Ballmer & Pratt 1988
C. (M.) siva	Cupressaceae	2	y	0*	Ballmer & Pratt 1988
C. (M.) loki	Cupressaceae	2	y	0*	Ballmer & Pratt 1988
C. (M.) thornei	Cupressaceae	2	y	0*	Ballmer & Pratt 1988
C. (M.) cedrosensis	Cupressaceae ?	1?	?	(0*)	Brown & Faulkner 1989
C. (M.) gryneus	Cupressaceae	2	y, i	0*	Scott 1986
C. (M.) hesseli	Cupressaceae	1?	y	(0*)	Scott 1986
C. (M.) johnsoni	Loranthaceae	2	–	0*	Ballmer & Pratt 1988
C. (M.) spinetorum	Loranthaceae	2	–	0*	Ballmer & Pratt 1988
C.(Ahlbergia) ferrea	Caprifoliaceae Ericaceae Rosaceae	5	i, f	0	Iwase 1954, Shirôzu & Hara 1974
C. (A.) haradai	Rutaceae	1?	f	0	Igarashi 1973
C. (Cyanophrys) goodsoni	Phytolaccaceae	1?	i, f	(0*)	Scott 1986
C. (Cy.) miserabilis	Fabaceae Caesalpiniaceae Asteraceae	5	i	(0*)	Scott 1986, Robbins, pers. comm.
C. (Cy.) amyntor	Ulmaceae Verbenaceae	4	y, i	(0*)	Kendall 1975, Robbins, pers. comm.
C. (Cy.) herodotus	Anacardiaceae Caprifoliaceae Boraginaceae Verbenaceae Asteraceae	5	i, f	(0*)	Robbins & Aiello 1982, Scott 1986
C. (Cy.) longula	Verbenaceae Asteraceae	4	i	(0*)	DeVries, pers. comm.
C. (Cy.) near pseudolongula [as *longula*]	Fabaceae Malvaceae Sterculiaceae Asteraceae (lab)	5	(i)	(0*)	Zikan 1956, Biezanko et al. 1974
C. (Cy.) remus	Fabaceae	2?	(i)	(0*)	Biezanko et al. 1966
Chalybs janias	Fabaceae	1?	–	?	DeVries, pers. comm.
Ch. hassan [as *janias*]	Fabaceae	2?	?	?	Hoffmann 1932
Michaelus vibidia	Bignoniaceae	?	i	?	Robbins & Aiello 1982
M. jebus	Fabaceae Mimosaceae	3	i, f	?	d'Araujo e Silva et al. 1967/68

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Oenomaus ortygnus	Annonaceae	2	i, f, e	2*	Hinton 1951, Kendall 1975
Olynthus narbal	Lecythidaceae	1?	i, e	3(*)	DeVries, pers. comm.
O. hypsea	Lecythidaceae	1?	i	(2*)	Nicolay 1982
Parrhasius m-album	Fagaceae Tiliaceae	4	?	0?	Scott 1986
P. polibetes	Euphorbiaceae Fabaceae	4	i	0?	Zikan 1956
P. selika	Fabaceae	1?	i	?	d'Araujo e Silva et al. 1967/68
Panthiades bitias	Mimosaceae Fabaceae Chrysobalanaceae Combretaceae Simaroubaceae Fagaceae, Euphorbiaceae, Sterculiaceae	5	y, i	3(*)	Kirkpatrick 1953, Callaghan 1982, DeVries, pers. comm.
P. hebraeus [as *cimelius*]	Fabaceae Rosaceae	4	(i)	(3*)	d'Araujo e Silva et al. 1967/68
Strymon melinus	Fabaceae Polygonaceae Cactaceae Fagaceae, Myricaceae, Juglandaceae, Cannabaceae, Moraceae, Crassulaceae, Rosaceae, Rutaceae, Zygophyllaceae, Rhamnaceae, Euphorbiaceae, Hypericaceae, Malvaceae, Ericaceae, Apocynaceae, Asclepiadaceae, Boraginaceae, Loasaceae, Scrophulariaceae, Bignoniaceae, Verbenaceae, Lamiaceae, Asteraceae, Liliaceae, Agavaceae, Poaceae, Arecaceae, Pinaceae (total 32 families)	5	y, i, f, e	?*(rud.)	Scott 1986, Ballmer & Pratt 1988
S. mulucha	Fabaceae Melastomataceae Malvaceae Bignoniaceae Amaryllidaceae Orchidaceae	5	i, f	?	d'Araujo e Silva et al. 1967/68
S. avalona	Fabaceae Polygonaceae	4	y, i	?*	Ballmer & Pratt 1988
S. oribata [as *arenicola*]	Fabaceae	1?	f	?	Jörgensen 1934
S. bebrycia	Fabaceae Sapindaceae	4	f, e	?(*)	Scott 1986, Robbins, pers. comm.
S. istapa [as *columella*]	Malvaceae	3/4?	i	?*	Ballmer & Pratt 1988
S. yojoa	Fabaceae Crassulaceae Gesneriaceae Begoniaceae Malvaceae, Alstroemeriaceae, Orchidaceae	5	i, f, e	0/2?*	Kendall 1975 Robbins & Aiello 1982, DeVries, pers. comm.
S. rufofusca	Malvaceae	3	y, i	?(*)	Kendall 1975
S. albata	Malvaceae Flacourtiaceae	4	y, i	?(*)	Kendall 1975, Robbins, pers. comm.

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Strymon martialis	Ulmaceae Simaroubaceae	5	y, i, f	?(*)	Scott 1986
S. acis	Euphorbiaceae	2	i, f	?*(rud.)	Scott 1986
S. alea	Euphorbiaceae	1?	i, f	?(*)	Scott 1986
S. bazochii	Verbenaceae Lamiaceae	4	i, f	?(*)	Scott 1986
S. gabatha	Bromeliaceae	2	i, f, e	?	DeVries, pers. comm.
S. legota	Bromeliaceae	3	f	?	Fonesca 1934
S. oreala	Bromeliaceae	2	f, e	3(*)	Zikan 1956
S. ziba [as *basilides*]	Bromeliaceae Haemodoraceae Musaceae Strelitziaceae	5	i, f, e	0?*	Robbins & Aiello 1982, Robbins, pers. comm.
Electrostrymon angelia	Anacardiaceae	1?	y	?	Scott 1986
E. mathewi	Bignoniaceae	3	i	0?	Robbins & Aiello 1982
Calycopis cecrops	Anacardiaceae Myricaceae Euphorbiaceae	5	i	(0)	Scott 1986
C. isobeon ssp. of *cecrops?*	Euphorbiaceae Boraginaceae Sapotaceae detritus	5	i, f	(0)	Scott 1986, Robbins, pers. comm.
C. chacona ssp. of *cecrops?*	Ulmaceae	1?	?	?	Biezanko et al. 1966
C. beon	??	?	(i, f)	0	Malicky 1969b
Symbiopsis tanais	Fabaceae	2?	y	0	DeVries, pers. comm.
Tmolus echion	Fabaceae Combretaceae Simaroubaceae Anacardiaceae Malpighiaceae, Solanaceae, Boraginaceae, Acanthaceae, Gesneriaceae, Verbenaceae, Lamiaceae, Bromeliaceae	5	i, f	3*	Ehrlich & Raven 1964, Robbins & Aiello 1982
T. mutina	Lecythidaceae	1?	i	(3*)	DeVries, pers. comm.
Ministrymon leda	Fabaceae	2	i	?*	Ballmer & Pratt 1988
M. clytie	Fabaceae	2	(i)	?(*)	Scott 1986
M. azia	Mimosaceae Fabaceae Malvaceae ?	3/4?	i	(3*)	Scott 1986, Robbins, pers. comm.
Phaeostrymon alcestis	Sapindaceae	1?	y	?	Scott 1986
Hypostrymon critola	Celastraceae	1?	?	?	Scott 1986
Erora laeta	Fagaceae Betulaceae Corylaceae Salicaceae (lab) Rhamnaceae ?	5	f	0	Klots & dos Passos 1981, Scott 1986
E. quaderna	Fagaceae	2	f	0	Klots & dos Passos 1981

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Iaspis castitas [as *talyra*]	Sterculiaceae	1?	y	3(*)	Kirkpatrick 1953
Ipidecla miranda	Anacardiaceae	1?	?	?	Kaye 1940
"Thecla" phydela	Asteraceae	2	y	0	Zikan 1956
"Th." hesperitis	Combretaceae Bignoniaceae Bromeliaceae	5	i, f	0?	Robbins & Aiello 1982, Robbins, pers. comm.
"Th." hemon	Fabaceae Sterculiaceae	4	y	0?	Robbins & Aiello 1982
"Th." thyrea	??	?	?	0?	Zikan 1956
"Th." hisbon	Fabaceae Lecythidaceae	4	i	0	DeVries, pers. comm.
"Th." lisus	Fabaceae Chrysobalanaceae Meliaceae Sterculiaceae	5	?	0	Kirkpatrick 1953, Zikan 1956
"Th." umbratus	Sapotaceae	3	y	?	Kendall 1975,
"Th." mycon	Fabaceae Sapindaceae	4	y	?	Muyshondt 1974
"Th." keila	Fabaceae	1?	y, i	?	DeVries, pers. comm.
"Th." tympania	Sterculiaceae Melastomataceae	4	y, f	3(*)	Kirkpatrick 1953
"Th." syedra	Sapindaceae	1?	?	?	Matta 1929
"Th." emessa	Malpighiaceae	1?	y	3(*)	DeVries, pers. comm.
"Th." azaria	Begoniaceae	2	i	0	Zikan 1956

Polyommatini: Candaliditi

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Candalides gilberti	Loranthaceae ?	?	?	(2**)	Common & Waterhouse 1981
C. margarita	Loranthaceae Sapindaceae	4	y, i	2**	Common & Waterhouse 1981
C. helenita	Lauraceae Euphorbiaceae Sterculiaceae	5	(y, i)	(2**)	Common & Waterhouse 1981, Valentine & Johnson 1988
C. absimilis	Fabaceae Caesalpiniaceae Proteaceae Sapindaceae Sterculiaceae Flagellariaceae	5	y, i	(2**)	Common & Waterhouse 1981
C. consimilis	Cunoniaceae Sapindaceae Araliaceae	5	y, i	(2**)	Common & Waterhouse 1981
C. cyprotus	Fabaceae Proteaceae	4	(y, i)	(2)**	Common & Waterhouse 1981, Atkins & Heinrich 1987
C. erinus	Lauraceae	2?	?	2/3**	Common & Waterhouse 1981
C. geminus	Lauraceae Cassythaceae	3	i	(2/3)**	Edwards 1980, Common & Waterhouse 1981

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Candalides acastus	Lauraceae	2?	i	(2/3**)	Common & Waterhouse 1981
C. hyacinthinus	Lauraceae	2	y, i	(2/3**)	Common & Waterhouse 1981
C. xanthospilos	Thymelaeaceae	2	?	3**	Common & Waterhouse 1981
C. heathi	Thymelaeaceae Scrophulariaceae Plantaginaceae Myoporaceae Lamiaceae	5	?	2**	Common & Waterhouse 1981
C.(Adaluma) urumelia	Rutaceae	2	-	3**	Edwards 1980
C. (Nesolycaena) albosericea	Rutaceae	2	i	0(**?)	Common & Waterhouse 1981
Lycaenesthiti					
Anthene emolus	Caesalpiniaceae Mimosaceae Fabaceae Combretaceae Meliaceae, Sapindaceae, Verbenaceae ?	5	y	4**	Corbet & Pendlebury 1978, Fiedler & Maschwitz 1989b
A. seltuttus	Caesalpiniaceae Fabaceae Lythraceae Myrtaceae Sapindaceae Sterculiaceae	5	y	4**	Common & Waterhouse 1981, Valentine & Johnson 1988
A. lycaenina	Mimosaceae Anacardiaceae	4	y, f	2/3**	Bell 1915, Hinton 1951
A. lycaenoides	Caesalpiniaceae Fabaceae Mimosaceae Sapindaceae Verbenaceae	5	(y)	4**	Common & Waterhouse 1981, Valentine & Johnson 1988
A. ligures	Ulmaceae	2	?	0?	Jackson 1937
A. definita	Mimosaceae Caesalpiniaceae Fabaceae Myricaceae Crassulaceae, Rosaceae, Anacardiaceae, Sapindaceae, Melianthaceae, Poaceae ??	5	y, i, f	2**	Clark & Dickson 1971
A. uzungwae	Escalloniaceae	1?	?	(2**)	Kielland 1990
A. lemnos	Euphorbiaceae	2	-	(2)**	Clark & Dickson 1971
A. indefinita	Euphorbiaceae Rubiaceae	4	y	(2**)	van Someren 1974, Sevastopulo 1975
A. pitmani	Mimosaceae	3	y	3**	Jackson 1937, Sevastopulo 1975
A. lunulata	Mimosaceae Caesalpiniaceae Combretaceae	5	y	3**	Hinton 1951, Kielland 1990
A. amarah	Mimosaceae	3	y	3**	Clark & Dickson 1971, Milton 1990

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Anthene larydas	Mimosaceae Caesalpiniaceae Hypericaceae ?	3	y	3**	Clark & Dickson 1971, Sevastopulo 1975, Ackery & Rajan 1990
A. princeps	Mimosaceae	3	y	0?	Jackson 1937
A. butleri	Crassulaceae	3	y, i, f, e	(2)**	Clark & Dickson 1971, van Someren 1974
A. talboti	Mimosaceae	2	y, i	(2)**	Clark & Dickson 1971
A. otacilia	Mimosaceae	3	y	3**	Clark & Dickson 1971, Kielland 1990
A. hodsoni	Mimosaceae	2?	y, e (galls)	3(**)	van Someren 1974
A. lysicles	Mimosaceae	2?	(y)	(3**)	Ackery & Rajan 1990
A. levis	*Crematogaster* regurgitations ?	–	?	4**	Jackson 1937, Hinton 1951, Ackery & Rajan 1990
A. crawshayi	Mimosaceae Caesalpiniaceae	3	y	3**	Jackson 1947, Hinton 1951
A. liodes	Myricaceae Combretaceae Anacardiaceae Sapindaceae	5	?	3**	Hinton 1951, Sevastopulo 1975
A. ? alberta	??	?	?	3/4(**?)	Ackery & Rajan 1990
A. sylvanus	??	?	?	3**	Hinton 1951
A. lachares	??	?	?	3**	Hinton 1951
A. flavomaculatus	??	?	?	3*(*)	Hinton 1951
A. rubricinctus	Fabaceae	1?	i	3(**)	Farquharson 1922
A. (Cupidesthes) wilsoni	Mimosaceae ?	3?	?	4	Jackson 1937
Triclema lamias	Sapotaceae ? Coccidae ?	?	y	(4*)*	Jackson 1947, Hinton 1951
T. ituriensis	Loranthaceae	2?	?	(3**)	Sevastopulo 1975
T. lucretilis	??	?	y	3(*)	Hinton 1951
T. nigeriae	Mimosaceae	2	y, e	4**	Jackson 1937, Hinton 1951
Neurypexina lyzianus	??	?	?	3(**)	Ackery & Rajan 1990
Niphanditi					
Niphanda fusca	Fagaceae + *Camponotus* regurgitations	2	?	4**	Pierce & Elgar 1985, Hama et al. 1989
Polyommatiti					
Cupidopsis section					
Cupidopsis cissus	Fabaceae	3	i, f, e	2/3**	Clark & Dickson 1971
C. iobates	Fabaceae	3	i, f	(2)**	Clark & Dickson 1971
Nacaduba section					
Petrelaea sichela	Fabaceae ?	?	?	?	Clark & Dickson 1971
Nacaduba sinhala	Sapotaceae	2?	i	2**	Bell 1915, Hinton 1951, Sevastopulo 1973
N. pactolus	Mimosaceae	2	y	2**	Bean 1964
N. beroe	Mimosaceae	2	y	(2**)	Bean 1964

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Nacaduba berenice	Proteaceae Sapindaceae Sterculiaceae	5	y, i	3**	Common & Waterhouse 1981
ssp. *plumbeomicans*	Mimosaceae	3?	y, i	2**	Hinton 1951
N. kurava	Sapindaceae Myrsinaceae	5	y, i	(2**)	Common & Waterhouse 1981, Valentine & Johnson 1988
ssp. *perusia*	Dipterocarpaceae	2?	(y)	(2**)	Sevastopulo 1973
N. normani	Fabaceae Sapindaceae Sterculiaceae	5	y	3(**)	Pan & Morishita 1990
N. biocellata	Mimosaceae	2	y, i	3**	Common & Waterhouse 1981
Prosotas dubiosa	Mimosaceae Proteaceae Sapindaceae	5	y, i	2/3**	Common & Waterhouse 1981, Cassidy 1990
P. felderi	Mimosaceae Proteaceae Sapindaceae	5	y, i	(2**)	Common & Waterhouse 1981, Hawkeswood 1988
P. nora	Mimosaceae Fabaceae	3	i	2**	Bell 1915, Hinton 1951, Larsen 1987, Bean 1988
Catopyrops florinda	Caesalpiniaceae Ulmaceae	4	?	3**	Common & Waterhouse 1981
Erysichton lineata	Proteaceae Sapindaceae Boraginaceae	5	i	(3)**	Common & Waterhouse 1981, Ballmer & Pratt 1988
E. palmyra	Loranthaceae	1	i	(3**)	Common & Waterhouse 1981
Neolucia agricola	Fabaceae	3	i, f, e	(0)	Common & Waterhouse 1981
N. hobartensis	Epacridaceae	2	y, i	0(*?)	Common & Waterhouse 1981
N. mathewi	Fabaceae Epacridaceae	4	y, i	(0)	Common & Waterhouse 1981
Theclinesthes onycha	Cycadaceae	3	y	2/3**	Common & Waterhouse 1981
Th. miskini	Mimosaceae Fabaceae Myrtaceae Sapindaceae	5	y	3**	Common & Waterhouse 1981
Th. scintillata	Mimosaceae Proteaceae Sapindaceae	5	i, f	(3**)	Common & Waterhouse 1981
Th. albocincta	Euphorbiaceae	2	y, i, f	3**	Grund & Sibatani 1975
Th. hesperia	Euphorbiaceae	2	(y, i)	(3**)	Common & Waterhouse 1981
Th. serpentata	Chenopodiaceae	3	?	(2/3**)	Common & Waterhouse 1981
Th. sulpitius	Chenopodiaceae	3	?	2/3**	Samson 1987
Danis danis	Rhamnaceae	1?	–	(3*)	Common & Waterhouse 1981
D. hymetus	Rhamnaceae	1?	–	(3)*	Common & Waterhouse 1981, Ballmer & Pratt 1988
D. cyanea	Mimosaceae	2	?	3*	Common & Waterhouse 1981
D. schaeffera	Connaraceae	1?	?	(3*)	Seki et al. 1991
Discolampa ethion	Rhamnaceae	2	–	0?	Bell 1915, Hinton 1951, Sevastopulo 1973

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Jamides section					
Jamides bochus	Fabaceae Mimosaceae	3	y, i	2**	Matsuoka 1976, Norman 1976 Johnston & Johnston 1980
J. celeno	Caesalpiniaceae Fabaceae Meliaceae	5	y, i	2**	Corbet & Pendlebury 1978, Eliot 1980, pers. obs.
J. pura	Fabaceae Caesalpiniaceae	3	y, i	(2**)	Seki et al. 1991, Nässig, pers. comm.
J. caeruleus	Caesalpiniaceae	3?	y, i	(2**)	Nässig, pers. comm.
J. elpis	Zingiberaceae	3	i	2?(**)	Bell 1915, Sevastopulo 1973
J. alecto	Zingiberaceae	3	i	(2**)	Norman 1976, Seki et al. 1991
J. aleuas	Sapindaceae	2?	?	(2**)	Common & Waterhouse 1981
J. phaseli	Fabaceae	3	y, i, e	2**	Common & Waterhouse 1981
J. cyta	Myrtaceae	2?	i, e	(2?)**	Kirton & Kirton 1987
Catochrysops strabo	Fabaceae + ??	3/4?	i	3(**)	Bell 1915, Corbet & Pendlebury 1978
C. panormus	Fabaceae	2	y, i	3**	Common & Waterhouse 1981
Lampides boeticus	Fabaceae Cistaceae (ov.) Bignoniaceae (ov.)	3/4?	i, f, e	2**	Corbet & Pendlebury 1978, Martín 1984, Thomas & Mallorie 1985, Pelzer 1991
Uranothauma section					
Uranothauma nubifer	Mimosaceae	2	y	0	Jackson 1937
U. delatorum	Mimosaceae	2	y	0	Jackson 1937
U. falkensteini	Mimosaceae	2	y	0?**	Jackson 1937
U. vansomereni	Mimosaceae	2	(y)	?	Sevastopulo 1975
U. confusa	Escalloniaceae (lab)	1?	(y)	?	Kielland 1990
U. crawshayi	Escalloniaceae (lab)	1?	(y)	?	Kielland 1990
U. uganda	Escalloniaceae ?	?	(y)	?	Kielland 1990
U. cuneatum	Myricaceae (lab)	1?	(y)	?	Kielland 1990
U. heritsia	Euphorbiaceae	1?	y	0	Jackson 1937
Phlyaria cyara	Mimosaceae	1?	y	0?**	Jackson 1937
Cacyreus lingeus	Lamiaceae Geraniaceae	4	y, i, f, e	0?*	Clark & Dickson 1971, Sevastopulo 1975
C. virilis	Lamiaceae	3	i	0?*	Clark & Dickson 1971
C. darius	Lamiaceae	2?	(i)	0?	Ackery & Rajan 1990
C. palemon	Geraniaceae	3	i, f, e	0	Clark & Dickson 1971
C. marshalli	Geraniaceae	3	i, f, e	0	Clark & Dickson 1971
C. dicksoni	Geraniaceae	3	i, f, e	0	Clark & Dickson 1971
C. niebuhri	Geraniaceae	2	(i, f, e)	(0)	Larsen 1984
Harpendyreus notobia	Lamiaceae	2	i	0?*	Clark & Dickson 1971
H. tsomo	Lamiaceae	4	(i, f)	?	Pennington et al. 1978
ssp. *noquasa*	Rosaceae		(i, f)	?	Migdoll 1988

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Leptotes section					
Leptotes pirithous	Fabaceae Mimosaceae Caesalpiniaceae Plumbaginaceae	5	y, i, f, e	2**	Claassens & Dickson 1980, Martín 1984, Migdoll 1988, Jutzeler, pers. comm.
	Rosaceae, Verbenaceae, Bignoniaceae, Lythraceae ?				
L. plinius	Mimosaceae Fabaceae Plumbaginaceae	5	i, f	2/3**	Warnecke 1932/33, Sevastopulo 1973
L. pulchra	Mimosaceae Fabaceae	3	(i, f)	(2**)	Stempffer 1967
L. brevidentatus	Fabaceae Plumbaginaceae	4	i, f, e	2**	Clark & Dickson 1971, Ackery & Rajan 1990
L. jeanneli	Fabaceae	3?	(i, f)	(2)**	Clark & Dickson 1956, Ackery & Rajan 1990
L. webbianus	Fabaceae	3	y, i, f	(1)**	Bacallado 1976, Martín 1982, Schurian, pers. comm.
L. mandersi	Fabaceae Caesalpiniaceae	3	(y, i)	(2**?)	Ackery & Rajan 1990
L. cassius	Fabaceae Plumbaginaceae Malpighiaceae	5	i, f	3**	Downey & Allyn 1979
L. marina	Fabaceae Mimosaceae Plumbaginaceae Rosaceae	5	i, f	3**	Ballmer & Pratt 1988
Castalius section					
Castalius rosimon	Rhamnaceae	2	y	2**	Bell 1915, Corbet & Pendlebury 1978
C. (Tuxentius) cretosus	Rhamnaceae	2	y	(2)**	Jackson 1937, van Someren 1974
C. (T.) melaena	Rhamnaceae Fabaceae ?	2/4?	–	(2)**	Clark & Dickson 1971, Ackery & Rajan 1990
C. (T.) calice	Rhamnaceae Fabaceae	4	–	(2)**	Clark & Dickson 1971, Ackery & Rajan 1990
C. (T.) interruptus	Rhamnaceae	2	–	(2**)	Larsen 1984
C. (T.) margaritaceus	Rhamnaceae	2	?	(2**)	Sevastopulo 1975
C. (Caleta) decidia	Rhamnaceae	2	y	2**	Hinton 1951
Tarucus ananda	Rhamnaceae Loranthaceae Oleaceae	4	?	3/4**	Bell 1915, Hinton 1951
T. waterstradti	Rhamnaceae Myrtaceae	4	?	3/4**	Maschwitz et al. 1985b
T. callinara	??	?	?	3(**)	Elfferich, pers. comm.
T. nara	Rhamnaceae	2	?	3/4**	Bell 1915, Sevastopulo 1941, Larsen 1987
T. rosaceus	Rhamnaceae	2	y	3**	Chapman & Buxton 1919

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Tarucus balkanicus	Rhamnaceae	3	?	3*(*)	Wiltshire 1945, 1948
T. theophrastus	Rhamnaceae	2	y	3**	Baz 1988
T. sybaris	Rhamnaceae	2	–	3(**)	Clark & Dickson 1971, Ackery & Rajan 1990
T. grammicus	Rhamnaceae	2	?	(2**)	Sevastopulo 1975
T. thespis	Rhamnaceae Saxifragaceae	4	y	3**	Dickson 1944
T. bowkeri	Rhamnaceae	2	–	(2)**	Clark & Dickson 1971
T. ungemachi	Rhamnaceae	2	?	(2**)	Sevastopulo 1975
T. kiki	Rhamnaceae	2	?	(2**)	Ackery & Rajan 1990
Zintha hintza	Rhamnaceae	2	y	2/3**	Clark & Dickson 1971, van Someren 1974
Zizeeria section					
Zizina otis	Mimosaceae Fabaceae Zygophyllaceae	5	y, i	3**	Corbet & Pendlebury 1978, Seki et al. 1991
Z. labradus	Fabaceae	3	y, i, f	3**	Common & Waterhouse 1981
Z. antanossa	Fabaceae	3	y, i	(3)**	Clark & Dickson 1971
Zizeeria karsandra	Fabaceae Amaranthaceae Molluginaceae Polygonaceae Oxalidaceae Zygophyllaceae	5	y, i, f	2/3**	Common & Waterhouse 1981, Larsen 1990
Z. knysna	Fabaceae Amaranthaceae Chenopodiaceae Oxalidaceae Zygophyllaceae Euphorbiaceae	5	y	3**	Clark & Dickson 1971, Ackery & Rajan 1990
Z. maha	Oxalidaceae	2	(y, i)	3**	Shields 1984, Shirôzu & Hara 1974
Famegana alsulus	Fabaceae	3	y, i	3**	Common & Waterhouse 1981
Actizera lucida	Fabaceae Oxalidaceae	4	i, f	(2)**	Clark & Dickson 1971
A. stellata	Fabaceae Oxalidaceae	4	y, i, f	(2)**	Clark & Dickson 1971, Sevastopulo 1975
Zizula hylax	Fabaceae Oxalidaceae Zygophyllaceae Acanthaceae Verbenaceae	5	y, i, f, e	3**	Bell 1915, Warnecke 1932/33, Clark & Dickson 1971, Ackery & Rajan 1990
Brephidium metophis	Chenopodiaceae	2?	e	(2)**	Clark & Dickson 1971
B. exilis	Chenopodiaceae Aizoaceae Amaranthaceae Solanaceae ?	5	i, f	3**	Fernández Haeger 1988
B. isophthalma	Chenopodiaceae Batidaceae	4	(i, f)	3**	Harvey & Longino 1989
Oraidium barberae	Chenopodiaceae	1?	?	(2**)	Migdoll 1988

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Cupido section					
Everes lacturnus	Fabaceae	3	i, f	2*(*?)	Shirôzu & Hara 1974, Corbet & Pendlebury 1978
E. huegelii	Fabaceae	3	y, i, e	(2*?)	Jones 1938
E. argiades	Fabaceae Cannabaceae ?	3/4	i, f	2**	Iwase 1954
E. amyntula	Fabaceae	3	i, f, e	2**	Ballmer & Pratt 1988
E. comyntas	Fabaceae	3	y, i, f, e	2**	Warnecke 1932/33, Ballmer & Pratt 1988
E. alcetas	Fabaceae	3	i, f	(2)**	SBN 1987
E. decoloratus	Fabaceae	2/3	(i, f)	(2**)	Higgins & Riley 1978
E. pontanini	*Boea*	2?	i	(2)**	Koiwaya 1989
E. (Tongeia) fischeri	Crassulaceae	3	–	3*	Iwase 1954
E. (T.) hainani	Crassulaceae	2	?	(2*)	Uchida 1985
E. (T.) ion	Crassulaceae	2	?	(2)*	Koiwaya 1989
E. (Talicada) nyseus	Crassulaceae	3	e	1(*)	Bell 1915, Larsen 1987, Elfferich, pers. comm.
Cupido minimus	Fabaceae	3	i, f, e	2*	Baylis & Kitching 1988
C. lorquinii	Fabaceae	3	i, f	3*	Munguira & Martín 1989, Devarenne 1990
C. osiris	Fabaceae	2?	i, f	3**	SBN 1987
Pithecops corvus	Fabaceae Rubiaceae	4	(i)	(3**)	Corbet & Pendlebury 1978
P. fulgens	Fabaceae	2?	y, i	3*(*)	Ejima et al. 1978
Azanus jesous	Mimosaceae Fabaceae	3	y, i, f, e	3**	Bell 1915, Migdoll 1988
A. ubaldus	Mimosaceae	2	i, f	3**	Hinton 1951
A. uranus	Mimosaceae	2	i, f	3**	Hinton 1951
A. moriqua	Mimosaceae	2	i, f, e	(3)**	Clark & Dickson 1971
A. occidentalis mirza	Mimosaceae Sapindaceae	4	i, f	(3)**	Clark & Dickson 1971
A. natalensis	Mimosaceae	2	y, i, f, e	3**	Clark & Dickson 1971
A. isis	Mimosaceae	2?	y	(3**)	van Someren 1974
Eicochrysops messapus	Fabaceae Mimosaceae Santalaceae	5	i, f	3**	Sevastopulo 1975, Claassens & Dickson 1980
Ei. hippocrates	Polygonaceae	3	i, f	(3)**	Clark & Dickson 1971
Ei. nandianus	??	?	f	(3**)	Jackson 1937
Lycaenopsis section					
Neopithecops zalmora	Rutaceae	2	y, i, e	2**	Bell 1915, Hinton 1951
N. lucifer	Rutaceae	2	(y, i)	2**	Common & Waterhouse 1981
Megisba strongyle	Sapindaceae Euphorbiaceae Mimosaceae (lab)	5	y, i	(2)**	Lambkin & Samson 1989
M. malaya	Sapindaceae Euphorbiaceae	4	(y, i)	(2**)	Corbet & Pendlebury 1978

Table <u>17</u> *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Udara albocaerulea	Rosaceae Symplocaceae Aquifoliaceae Caprifoliaceae	5	i, f	(2)*	Iwase 1954, Shirôzu & Hara 1974
U. dilecta	Fagaceae	1?	?	?	Seki et al. 1991
U. (Vaga) blackburni	Mimosaceae Urticaceae Sapindaceae Rubiaceae	5	i, f	0	Scott 1986
Actyolepis puspa	Fabaceae Caesalpiniaceae Mimosaceae Rosaceae Combretaceae, Sapindaceae, Malpighiaceae, Euphorbiaceae, Ericaceae	5	(i, f)	2*(*)	Shirôzu & Hara 1974, Corbet & Pendlebury 1978, Johnston & Johnston 1980
Celastrina argiolus	Fabaceae Ranunculaceae Polygonaceae Hamamelidaceae Fagaceae, Moraceae, Saxifragaceae, Rosaceae, Lythraceae, Anacardiaceae, Hippocastanaceae, Celastraceae, Rhamnaceae, Araliaceae, Aquifoliaceae, Cornaceae, Ericaceae, Oleaceae, Caprifoliaceae, Lamiaceae, Asteraceae etc.	5	i, f	2**	Scott 1986, Ballmer & Pratt 1988, Jutzeler 1990a
C. ebenina	Rosaceae	1	y, i, f	2(**)	Scott 1986
C. sugitanii	Hippocastanaceae Cornaceae	4	i, f	2*(*)	Iwase 1954, Shirôzu & Hara 1974, Eliot & Kawazoé 1983
C. gigas	Rosaceae	1?	–	0(*)?	Jones 1938
C. huegelii	Rosaceae	1?	–	0(*)?	Jones 1938
C. oreas	Rosaceae	1?	–	0(*)?	Norman 1950, 1976
C. lavendularis	Fabaceae	3	(y)	(2**)	Uchida 1984
Glaucopsyche section *Glaucopsyche*					
lygdamus	Fabaceae	3	i, f	3**	Ballmer & Pratt 1988
G. piasus	Fabaceae	2	i, f	3**	Ballmer & Pratt 1988
G. lycormas	Fabaceae	2?	i, f	3**	Iwase 1954
G. alexis	Fabaceae	3	i, f	3**	SBN 1987
G. paphos	Fabaceae	1?	(i)	(3**)	Parker 1983
G. melanops	Fabaceae	3	i, f	3**	Martín 1981
Maculinea arion	Lamiaceae	2	i, f	4*	SBN 1987
M. arionides	Lamiaceae	2?	i, f	4(*)	Iwase 1953 & 1954
M. teleius	Rosaceae	2	i, f, e	4*	SBN 1987
M. nausithous	Rosaceae	1	i, f, e	4*	SBN 1987
M. alcon	Gentianaceae	2	i, f, e	4*	SBN 1987
M. rebeli	Gentianaceae	2	i, f, e	4*	SBN 1987
Iolana iolas	Fabaceae	2	i, f, e	2*	SBN 1987, Devarenne 1990
I. alfierii	Fabaceae	1	i, f	(2*)	Larsen 1990
Sinia divina	Fabaceae	1?	i, f	3**	Iwase 1954

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Turanana panagaea	Fabaceae (ov.)	1?	?	(3**)	Schurian & Eckweiler, pers. comm.
T. cytis	Fabaceae ?	1?	?	(3**)	Schurian & Eckweiler, pers. comm.
Pseudophilotes					
baton	Lamiaceae	3	i, f	2**	SBN 1987
Ps. panoptes	Lamiaceae	3	i, f	(2**)	Nel 1982
Ps. schiffermuelleri	Lamiaceae	2/3	(i, f)	(2)**	Higgins & Riley 1978
Ps. barbagiae	Lamiaceae ?	2?	?	(2**)	de Prins & van der Poorten 1982
Ps. abencerragus	Lamiaceae Fabaceae	4	(i, f)	(2**)	Thomas & Mallorie 1985, Devarenne 1990
Ps. bavius	Lamiaceae	2	i, e	2*(*)	Thomas & Mallorie 1985, König 1988
Ps. sinaicus	Lamiaceae	2	y, i	(2**)	Larsen 1990
Euphilotes enoptes	Polygonaceae	2	y, i, f	3**	Langston & Comstock 1966, Ballmer & Pratt 1988
Eu. mojave	Polygonaceae	2	y, i, f	(3)**	Ballmer & Pratt 1988
Eu. rita	Polygonaceae	2	y, i, f	3**	Ballmer & Pratt 1988
Eu. battoides	Polygonaceae	2	y, i, f	3**	Ballmer & Pratt 1988
Eu. bernardino	Polygonaceae	2	(y, i)	3**	Mattoni 1989
Eu. spaldingi	Polygonaceae	2	y, i, f	(3**)	Scott 1986
Philotiella speciosa	Polygonaceae	1	y, i	(2)*	Ballmer & Pratt 1988
Philotes sonorensis	Crassulaceae	1	e	3**	Shields 1973, Ballmer & Pratt 1988
Scolitantides orion	Crassulaceae	2	e	3**	Chapman 1915c, SBN 1987
Euchrysops section					
Euchrysops cnejus	Fabaceae Mimosaceae	3	i, f, e	3**	Viehmeyer 1910a, Bell 1915, Common & Waterhouse 1981
Eu. osiris	Fabaceae Lamiaceae ?	3/4	y, i, f	3**	Clark & Dickson 1971
Eu. barkeri	Fabaceae Lamiaceae Bignoniaceae ?	5	y, i, e	3**	Clark & Dickson 1971, Ackery & Rajan 1990
Eu. malathana	Fabaceae Myrtaceae Bignoniaceae ?	4/5	y, i	3**	Clark & Dickson 1971, Sevastopulo 1975
Eu. dolorosa	Fabaceae Lamiaceae	4	y, f	1/2**	Clark & Dickson 1971, Henning 1983b
Eu. subpallida	Lamiaceae	2?	(y, i)	(2**)	Ackery & Rajan 1990
Eu. lois	Scrophulariaceae	2?	(y, i)	(2**)	Ackery & Rajan 1990
Eu. subdita crawshayinus	Boraginaceae	3	e	3**	Jackson 1937, Cripps 1947, Kielland 1990
Lepidochrysops					
lacrimosa	Fabaceae	1?	y	(3)**	Clark & Dickson 1971
L. ariadne	Fabaceae	2?	(i)	(3**)	Pennington et al. 1978
L. patricia	Verbenaceae	2	i	4*	Clark & Dickson 1971
L. (ssp?) parsimon	Lamiaceae	2?	(i)	(4*)	Sevastopulo 1975

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Lepidochr. plebeia	Verbenaceae	1?	?	(4*)	Migdoll 1988
L. vansoni	Verbenaceae	2?	(i)	(4*)	Pennington et al. 1978
L. peculiaris	Verbenaceae	2?	i, e	(4*)	Sevastopulo 1975
L. oreas	Selaginaceae	2	i	4*	Claassens & Dickson 1980
L. wykehami	Selaginaceae	2?	(i)	(4*)	Pennington et al. 1978
L. titei	Selaginaceae	2?	(i)	(4*)	Pennington et al. 1978
L. australis	Selaginaceae	2?	(i)	(4*)	Pennington et al. 1978
L. trimeni	Selaginaceae Fabaceae ?	4	y, i	4*	Clark & Dickson 1971
L. asteris	Selaginaceae Lamiaceae	4	i	(4)*	Clark & Dickson 1971
L. barnesi	Lamiaceae ?	?	(i)	(4*)	Pennington et al. 1978
L. ortygia	Selaginaceae Lamiaceae	4?	(i)	(4*)	Migdoll 1988
L. praeterita	Lamiaceae ?	?	(i)	(4*)	Pennington et al. 1978
L. jefferyi	Lamiaceae	2?	(i)	(4*)	Pennington et al. 1978
L. tantalus	Lamiaceae	2	(i)	(4*)	Migdoll 1988
L. swanepoeli	Lamiaceae	2?	(i)	(4*)	Pennington et al. 1978
L. grahami	Lamiaceae	2?	(i)	(4*)	Pennington et al. 1978
L. pephredo	Lamiaceae	2?	(i)	4(*)	Pennington et al. 1978
L. irvingi	Lamiaceae	2?	(i)	(4*)	Pennington et al. 1978
L. ignota	Lamiaceae	2	i, f	4*	Henning 1983a
L. letsea	Lamiaceae	1?	(i)	(4*)	Migdoll 1988
L. quassi [as *phasma*]	Lamiaceae	2	i	4*	Farquharson 1922, Chapman 1922
L. forsskali	Lamiaceae	2?	(i)	(4*)	Ackery & Rajan 1990
L. pittawayi	Lamiaceae	2?	(i)	(4*)	Ackery & Rajan 1990
L. variabilis	Selaginaceae Lamiaceae	4	i, e	4*	Cottrell 1965, Clark & Dickson 1971
L. ketsi	Selaginaceae Lamiaceae	4	i, e	(4)*	Cottrell 1965, Clark & Dickson 1971
L. robertsoni	Selaginaceae	2	i, (e)	4(*)	Claassens & Dickson 1980
L. dukei	Selaginaceae	2	i, e (galls)	(4)*	Cottrell 1965
L. bacchus	Selaginaceae	3	y, i, e	(4)*	Cottrell 1965, Clark & Dickson 1971
L. badhami	Geraniaceae (ov.)	?	(i)	(4*)	Pennington et al. 1978
L. puncticilia	Selaginaceae	3	y, i, e	(4*)	Cottrell 1965, Clark & Dickson 1971
L. methymna	Selaginaceae	3	y, i, (e)	4*	Cottrell 1965, Clark & Dickson 1971
L. victoriae	??	?	?	4(*)	Cripps 1947
L. longifalces	??	?	?	4(*)	Cottrell 1984
Oboronia punctatus	Zingiberaceae	2?	i	4(*)	Stempffer 1967
O. guessfeldtii	Zingiberaceae	2?	(i)	(4*)	Pennington et al. 1978
O. bueronica	Zingiberaceae	2?	(i)	(4*)	Kielland 1990
Athysanota ornata	Zingiberaceae ?	2?	?	(3/4*)	Kielland 1990

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Polyommatus section					
Chilades pandava	Fabales Cycadaceae	5	(y)	3**	Hinton 1951, Corbet & Pendlebury 1978
Ch. mindora [as *kiamurae*]	Cycadaceae	1?	y, e	(2**)	Wakabayashi & Yoshizaki 1967
Ch. lajus	Rutaceae + Aphididae!	3	y	2/3**	Bell 1915, Agarwala & Saha 1984
Ch. trochylus	Fabaceae Euphorbiaceae Boraginaceae	5	y, i, f, e	3**	Clark & Dickson 1971, Larsen 1990, Wasserthal, pers. comm.
Ch. parrhasius	Caesalpiniaceae Mimosaceae	3	i, f	3**	Larsen 1980, 1984
Ch. galba	Caesalpiniaceae	3	(i)	3(**)	Larsen & Nakamura 1983
Ch. kedonga	Mimosaceae (ov.)	2?	y, i	(3**)	van Someren 1974
Ch. eleusis	Mimosaceae	2?	(y, i)	(3**)	Ackery & Rajan 1990
Plebejus saepiolus	Fabaceae	2	i, f	(3)**	Ballmer & Pratt 1988
P. argus	Fabaceae Cistaceae Ericaceae Geraniaceae (lab) Lamiaceae ? Asteraceae ?	5	i	3/4**	Thomas 1985, pers. observ.
P. (Plebejides) martini	Fabaceae Ericaceae ?	2/4?	(y)	3**	Thomas & Mallorie 1985, Rojo de la Paz pers. comm.
P. (P.) hespericus	Fabaceae	2	(y)	3**	Munguira & Martín 1989, Bálint 1991
P. (P.) trappi	Fabaceae	2	y	3**	SBN 1987, Bálint 1991
P. (P.) sephirus	Fabaceae	2	y	3**	Bálint & Kertész 1990, pers. observ.
P. (P.) pylaon	Fabaceae	2	(y)	3(**)	Bálint & Kertész 1990, Bálint 1991
P. (P.) philbyi	Fabaceae	2	(y)	3(**)	Bálint & Kertész 1990, Bálint 1991
P. vogelii	Geraniaceae	1?	i	(3**)	Thomas & Mallorie 1985, Devarenne 1990
P. (Lycaeides) idas	Fabaceae Elaeagnaceae Cistaceae Empetraceae Ericaceae	5	y, i	3/4**	SBN 1987, Ballmer & Pratt 1988, Jutzeler 1989d, 1990b
P. (L.) melissa	Fabaceae	3	y, i	3**	Ballmer & Pratt 1988
P. (L.) argyrognomon	Fabaceae	3	i, f	3**	SBN 1987
P. (L.) subsolana	Fabaceae	3	y	3**	Iwase 1954, Hama et al. 1989
Plebejus (Icaricia) icarioides	Fabaceae	2	y, i, f	3**	Ballmer & Pratt 1988
P. (I.) acmon	Fabaceae Polygonaceae	4	y, i, f	3**	Ballmer & Pratt 1988
P. (I.) lupini	Polygonaceae	2	i	3**	Ballmer & Pratt 1988

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
P. (Icaricia) shasta	Fabaceae	3	y, i	3**	Emmel & Shields 1980
P. (I.) neurona	Polygonaceae	2	(y, i)	(3)**	Ballmer & Pratt 1988
P. (Plebulina)					
emigdionis	Chenopodiaceae Fabaceae ?	1/3?	–	3**	Scott 1986, Ballmer & Pratt 1988
P. (Vacciniina)					
optilete	Ericaceae	2	y, i	0	SBN 1987
P. (V.) loewii	Fabaceae	2	y, i	?	Larsen 1990, Schurian, pers. comm.
P. (V.) morgiana [as *hyrcana*]	Fabaceae (ov.)	2?	y	?	Eckweiler 1981
P. (V.) kwaja	Fabaceae	1?	?	?	Eckweiler, pers. comm.
P. (Kretania)					
psylorita	Fabaceae	1?	?	?	Hemmersbach 1989, Leigheb et al. 1990
Polyommatus (Albulina)					
orbitulus	Fabaceae	3	?	(2)**	SBN 1987
P. (Agriades)					
franklinii	Primulaceae	1?	e	0	Ballmer & Pratt 1988
P. (A.) glandon	Primulaceae	2/3	i	0	SBN 1987
P. (A.) zuellichi	Primulaceae	1	y, i	0	Munguira & Martín 1989a
P. (A.) aquilo	Saxifragaceae Diapensiaceae (ov.) Ericaceae (ov.) Fabaceae ?	5	i	0	Higgins & Riley 1978, Scott 1986, Klassen et al. 1989
P. (A.) pyrenaicus	Primulaceae	3	y, i	0	Chapman 1915a, Martín 1982
P. (A.) ergane	Primulaceae	1	y, i	0	Pljushtch 1989
P. (Aricia)					
agestis	Geraniaceae Cistaceae	4	y, i	3**	SBN 1987
P. (A.) artaxerxes	Geraniaceae Cistaceae	4	y, i	3**	SBN 1987
P. (A.) cramera	Geraniaceae Cistaceae	4	(i, f)	3**	Martín 1982, Thomas & Mallorie 1985
P. (A.) morronensis	Geraniaceae	2	y, i	3**	Munguira & Martín 1988
P. (A.) nicias	Geraniaceae	2	i, f	(3)**	SBN 1987
P. (A.) anteros	Geraniaceae	2	(i, f)	(3**)	Schurian, pers. comm.
P. (A.) isaurica	Geraniaceae	2	i, f	(3)**	Schurian, pers. comm.
P. (A.) hyacinthus	Geraniaceae	2	i	(3)**	Schurian & Rose 1991
P. (A.) vandarbani	Geraniaceae (ov.)	2?	(i)	(3**)	Schurian & Rose 1991
P. (A.) eumedon	Geraniaceae	2	i, f	3**	SBN 1987
P. (Agrodiaetus)					
damon	Fabaceae	2	i, f	3**	SBN 1987
P. (A.) humedasae	Fabaceae	2	(i)	(3)**	Manino et al. 1987
P. (A.) ainsae	Fabaceae	2?	?	(3**)	Martín 1982
P. (A.) dolus	Fabaceae	2	i, f	3**	Martín 1982
P. (A.) antidolus	Fabaceae ?	2	?	(3**)	Eckweiler, pers. comm.

Table **17** *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Polyommatus (Agrodiaetus)					
ripartii	Fabaceae	2	i, f	3**	Martín 1982
P. (A.) admetus	Fabaceae	2	(i, f)	(3)**	Higgins & Riley 1978
P. (A.) fabressei	Fabaceae	2?	?	(3**)	Martín 1982
P. (A.) carmon	Fabaceae (ov.)	2?	?	(3**)	Schurian, pers. comm.
P. (A.) turcicus	Fabaceae	2	?	(3**)	Schurian, pers. comm.
P. (A.) mithridates	Fabaceae ?	2	?	(3**)	Eckweiler, pers. comm.
P. (A.) baytopi	Fabaceae	2	?	(3**)	Schurian & Eckweiler, pers. comm.
P. (A.) hopfferi	Fabaceae	2	?	(3**)	Schurian, pers. comm.
P. (A.) firdussii	Fabaceae ?	2	?	(3**)	Eckweiler, pers. comm.
P. (A.) dama	Fabaceae ?	2	?	(3**)	Eckweiler, pers. comm.
P. (A.) hamadanensis	Fabaceae ?	2	?	(3**)	Eckweiler, pers. comm.
P. (A.) transcaspica	Fabaceae	2	?	(3**)	Schurian, pers. comm.
P. (A.) phyllis	Fabaceae (ov.)	1?	?	(3**)	Schurian, pers. comm.
P. (A.) actis	Fabaceae ?	1?	?	(3**)	Eckweiler & Görgner 1981
P. (A.) bogra ?	Fabaceae	1?	?	3(**)	Eckweiler, pers. comm.
P. (A.) glaucias	Fabaceae (ov.)	2	?	(3**)	Eckweiler, pers. comm.
P. (A.) thersites	Fabaceae	2	(y)	3**	Martín 1982
P. (A.) semiargus	Fabaceae	3	y, i	3**	SBN 1987
P. (A.) helena	Fabaceae	1?	y, i	(3**)	Brown 1977
P. (A.) corona	Fabaceae (ov.)	2?	?	(3**)	Schurian, pers. comm.
P. (A.) coelestina	Fabaceae (ov.)	2?	?	(3**)	Eckweiler & Görgner 1981, Schurian et al. 1991
P. (A.) diana	Fabaceae (ov.)	2	?	(3**)	Schurian et al. 1991, Eckweiler, pers. comm.
P. (A.) ellisoni	Fabaceae	2?	(y, i)	(2**)	Paulus & Rose 1971, Larsen 1974
P. (A.) myrrha	Fabaceae	2?	?	(3**)	Eckweiler & Görgner 1981, Schurian et al. 1991
P. (Lysandra)					
coridon	Fabaceae	2	–	3**	SBN 1987
P. (L.) hispana	Fabaceae	2	–	3**	Schurian 1989a
P. (L.) albicans	Fabaceae	2	–	3**	Schurian 1989a
P. (L.) ossmar	Fabaceae	2	–	3**	Schurian 1989a
P. (L.) corydonius	Fabaceae	2	–	(3)**	Schurian 1989a
P. (L.) bellargus	Fabaceae	2	–	3**	Thomas 1983
P. (L.) punctifera	Fabaceae	2	y	3**	Schurian & Thomas 1985
P. (L.) amandus	Fabaceae	2	(y, i)	3**	SBN 1987
P. (L.) escheri	Fabaceae	2	y, i	3**	Chapman 1915b, SBN 1987
P. (L.) dorylas	Fabaceae	1	i, f	3**	Munguira & Martín 1989b
P. (L.) golgus	Fabaceae	1	i, f	3**	Munguira & Martín 1989b
P. (L.) nivescens	Fabaceae	1	i, f	3**	Munguira & Martín 1989b
P. (L.) atlantica	Fabaceae	1?	(i, f)	(3**)	Thomas & Mallorie 1985
P. (Meleageria)					
daphnis	Fabaceae	2	–	3**	SBN 1987
P. (Polyommatus)					
icarus	Fabaceae Geraniaceae ?	3/4?	i	2/3**	Martín 1984, SBN 1987, Bálint, pers. comm.
P. eros	Fabaceae	3	y, i	2/3**	SBN 1987, Jutzeler 1989a

Table 17 *(continued)*

Species	Hostplant/ Foodsubstrate	Host range index	Preference	Myrmecophily	Reference(s)
Hemiargus ceraunus	Fabaceae Caesalpiniaceae Polygonaceae Marantaceae	5	y, i, f	3**	Ehrlich & Raven 1964, Ballmer & Pratt 1988
H. isola	Fabaceae Mimosaceae	3	y, i, f	3**	Scott 1986
H. thomasi	Caesalpiniaceae Sapindaceae Rubiaceae ?	4/5	i, f, e	(3**)	Scott 1986
H. ammon	Caesalpiniaceae	2?	(y, i)	(3**)	Riley 1975
H. hanno	Oxalidaceae	2?	(y, i)	(3**)	Barcant 1970

Note: The author has put special efforts into the accuracy and completeness of the above compilation. However, in view of the tremendous bulk of literature records that had to be evaluated, this listing will certainly not be free of errors, and the author takes full responsibility for all faults and inaccuracies that may have accumulated in the course of compilation. In particular, this holds for all hypothetical assignments. Any corrections and additions will be greatly acknowledged.

Table 18: Systematic synopsis of the hostplant taxa of the Lycaenidae and numbers of species certainly recorded to utilize them. See Table 17 for detailed records.

PTERIDOPHYTA			ROSIDAE	
Polypodiaceae	2		Cunoniaceae	1
			Grossulariaceae	1
			Saxifragaceae	4
CONIFEROPHYTINA .			Crassulaceae	19
Pinaceae	5		Escalloniaceae	3
Cupressaceae	7		Bruniaceae	1
			Rosaceae	50
CYCADOPHYTINA			Chrysobalanaceae	4
Cycadaceae	8			
			Fabales	321
MAGNOLIOPHYTINA			Proteaceae	15
MAGNOLIIDAE				
Annonaceae	3		Lythraceae	8
Lauraceae	13		Myrtaceae	29
Cassythaceae	1		Barringtoniaceae	1
Piperaceae	1		Punicaceae	5
			Lecythidaceae	7
			Melastomataceae	10
RANUNCULIDAE			Rhizophoraceae	3
Ranunculaceae	2		Combretaceae	27
			Rutaceae	8
CARYOPHYLLIDAE			Simaroubaceae	4
Molluginaceae	1		Anacardiaceae	19
Phytolaccaceae	1		Meliaceae	3
Batidaceae	1			
Aizoaceae	3		Sapindaceae	55
Cactaceae	1		Hippocastanaceae	4
Portulacaceae	1		Aceraceae	1
Chenopodiaceae	9		Melianthaceae	2
Amaranthaceae	4		Coriariaceae	1
Polygonaceae	58		Oxalidaceae	9
			Erythroxylaceae	1
Plumbaginaceae	5		Malpighiaceae	12
			Zygophyllaceae	21
			Geraniaceae	18
HAMAMELIDIDAE			Connaraceae	3
Hamamelidaceae	2			
Fagaceae	48		Celastraceae	3
Betulaceae	4		Hippocrateaceae	1
Corylaceae	3		Rhamnaceae	43
			Santalaceae	3
Myricaceae	5		Olacaceae	12
Juglandaceae	6		Loranthaceae	100
Casuarinaceae	1		Euphorbiaceae	37
			Thymelaeaceae	3
Ulmaceae	10		Elaeagnaceae	3
Moraceae	12			
Cannabaceae	1		Pittosporaceae	3
Urticaceae	2		Araliaceae	2
			Apiaceae	1

DILLENIIDAE
Theaceae	2
Hypericaceae	2
Ochnaceae	1
Dipterocarpaceae	1
Flacourtiaceae	1
Cistaceae	8
Salicaceae	6
Begoniaceae	2
Cucurbitaceae	3
Tiliaceae	4
Elaeocarpaceae	1
Sterculiaceae	18
Malvaceae	10
Ebenaceae	3
Styracaceae	1
Symplocaceae	3
Sapotaceae	9
Myrsinaceae	6
Primulaceae	5
Aquifoliaceae	3
Cornaceae	3
Ericaceae	19
Empetraceae	1
Epacridaceae	3
Diapensiaceae	1

LAMIIDAE
Caprifoliaceae	7
Oleaceae	12
Gentianaceae	2
Apocynaceae	1
Asclepiadaceae	1
Loganiaceae	3
Rubiaceae	18
Solanaceae	15
Convolvulaceae	4
Hydrophyllaceae	1
Boraginaceae	13
Loasaceae	1
Scrophulariaceae	3
Bignoniaceae	11
Acanthaceae	2
Gesneriaceae	1
Myoporaceae	1
Plantaginaceae	1
Verbenaceae	29
Lamiaceae	37
Selaginaceae	14

ASTERIDAE
Asteraceae	27

LILIIDAE
Dioscoreaceae	10
Smilacaceae	4
Agavaceae	2
Haemodoraceae	1
Alliaceae	2
Amaryllidaceae	1
Liliaceae	2
Alstroemeriaceae	1
Orchidaceae	5
Bromeliaceae	8
Musaceae	2
Strelitziaceae	1
Zingiberaceae	5
Marantaceae	1
Flagellariaceae	2
Poaceae	1

ARECIDAE
Arecaceae	3

Table 19: List of recorded ant-associations of the Lycaenidae (basically field observations, exceptional laboratory records = **lab**). Only records where the ants have been determined to genus level at least are incorporated. Systematic arrangement and nomenclature (first column), as well as presence of larval ant-organs and estimated degrees of myrmecophily (second column), are the same as in Table 17.

Third column: Associated ant genera or species according to the determinations given in the references cited. If reference is only made to a species-group within an ant genus, this is indicated by "**gr.**" following the species name. "**?**" inserted before the species name: uncertain species determinations. "**?**" following a species name: questionable determinations or doubtful records. Associations refer to caterpillars if not stated otherwise (**ad.** = adults, **ov.** = oviposition). Included are the few records where ants have been observed to behave indifferently towards the larvae (**indiff.**, e.g. Miletinae in ant-tended homopteran aggregations), or where attacks have been reported. Only those references are cited (fourth column) where appropriate information on the identity of associated ants is given (for further information see Table 17).

Lycaenid species	Degree of myrmecophily	Associated ants	Reference(s)
Poritiinae:			
Liptenini:			
Liptena undina	0/4?	*Crematogaster* sp.	Jackson 1937
Teratoneura isabellae	0/4?	*Crematogaster* sp.	Farquharson 1922
Deloneura ochrascens	0/4??	*Crematogaster* sp.	Jackson 1937
Iridana perdita marina	0/4?	*Crematogaster* sp.	Jackson 1937
Epitola (Aethiopana)			
honorius	3?	*Crematogaster* sp.	Farquharson 1922
E. (Epitola) urania	0/3?	*Crematogaster* sp.	Ackery & Rajan 1990
E. carcina	3?	*Crematogaster* sp.	Ackery & Rajan 1990
E. ceraunia	3?	*Crematogaster* sp.	Ackery & Rajan 1990
E. elissa	3?	*Crematogaster* sp.	Ackery & Rajan 1990
Miletinae:			
Miletini:			
Spalgis lemolea	0	*Crematogaster* sp. *Oecophylla longinoda* *Anaplocnemis* sp. (all indiff., at homopterans)	Cottrell 1984
Miletus chinensis	0/3?	*Dolichoderus bituberculatus* *Polyrhachis dives* (?)	Kershaw 1905
M. boisduvali	0/3?	*Dolichoderus* sp. *Polyrhachis* sp. (?)	Roepke 1919, Cottrell 1984
M. biggsii	0/4?	*Dolichoderus* sp.	Maschwitz et al. 1985a, 1988
M. symethus	0/4?	*Dolichoderus* sp.	Eliot 1980
Allotinus unicolor	0/3?	*Anoplolepis longipes* (indiff., ov.)	Maschwitz et al. 1985a, Fiedler & Maschwitz 1989c
A. subviolaceus	0	*Anoplolepis longipes* (indiff.)	Maschwitz et al. 1988
A. major	0	*Anoplolepis longipes* (indiff., ov.)	Kitching 1987

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Table 19 *(continued)*

Lycaenid species	Degree of myrmecophily	Associated ants	Reference(s)
Allotinus davidis	0	*Crematogaster difformis* (indiff.)	Maschwitz et al. 1985a
A. substrigosus	0	*Crematogaster* sp. (ad.) *Technomyrmex* sp. (indiff.)	Maschwitz et al. 1985a, 1988
A. apries	4?	*Myrmicaria lutea*	Maschwitz et al. 1988
Logania malayica	0?	*Leptothorax* sp. (indiff., ad.)	Maschwitz et al. 1988
Megalopalpus zymna	0	*Pheidole aurivillii* (indiff.)	Ackery 1990
Lachnocnema bibulus	0/4?	*Crematogaster* sp. *Pheidole* sp. (both indiff.)	Cottrell 1984
		Camponotus acvapimensis *C. maculatus*	Farquharson 1922, Cripps & Jackson 1940
L. brimo	0	*Camponotus* sp. (indiff.)	Ackery & Rajan 1990
Thestor dicksoni	4	*Anoplolepis custodiens*	Clark & Dickson 1971
Th. basutus	4	*Anoplolepis custodiens*	Clark & Dickson 1971
Th. obscurus	4?	*Anoplolepis custodiens*	Claassens & Dickson 1980
Euliphyra mirifica	4	*Oecophylla longinoda*	Cottrell 1984
Eu. leucyania	4	*Oecophylla longinoda*	Dejean 1991
Liphyra brassolis	4	*Oecophylla smaragdina*	Cottrell 1987
Aslauga lamborni	0^T	*Crematogaster* sp. (indiff.)	Ackery & Rajan 1990
A. vininga	$0^{(T)}$	*Crematogaster* sp. (indiff.)	Ackery & Rajan 1990
Curetinae:			
Curetis regula	$0/2?^T$	*Anoplolepis longipes*	DeVries 1984
Lycaeninae: Aphnaeini:			
Spindasis ella	3/4**	*Crematogaster castanea*	Clark & Dickson 1971
S. natalensis	4**	*Crematogaster castanea*	Clark & Dickson 1971
S. nyassae	4**	*Crematogaster* sp.	Hinton 1951
S. avriko	4(**)	*Pheidole* sp.	van Someren 1974
S. tavetensis	4(**)	*Pheidole* sp.	van Someren 1974
S. namaqua	4**	*Crematogaster* sp.	Henning 1983a
S. phanes	4**	*Crematogaster castanea*	Henning 1983a
S. lohita	3/4**	*Crematogaster* sp.	Hinton 1951
S. vulcanus	3/4**	*Crematogaster* sp. / *Pheidole quadrispinosa*	Hinton 1951
S. takanonis	4**	*Crematogaster laboriosa*	Cottrell 1984
Cigaritis zohra	4**	*Crematogaster laestrygon*	Rojo de la Paz 1990
C. allardi	3**	*Crematogaster auberti* *C. antaris* *C. scutellaris*	Rojo de la Paz 1990
C. (Apharitis) acamas	4**	*Crematogaster* sp.	Larsen & Pittaway 1982
C. (A.) myrmecophila	4**	*Crematogaster auberti* *Cataglyphis bicolor* ??	Hinton 1951
Axiocerses amanga	3**	*Camponotus niveosetosus*	Jackson 1937
A. harpax	4**	*Crematogaster* sp. *Pheidole* sp.	Jackson 1947, van Someren 1974

Table **19** *(continued)*

Lycaenid species	Degree of myrmecophily	Associated ants	Reference(s)
Axiocerses (Chloroselas)			
pseudozeritis	4**	*Crematogaster gerstaeckeri*	Jackson 1937
Phasis thero	4*	*Crematogaster peringueyi*	Clark & Dickson 1971
Ph. braueri	4*	*Crematogaster* sp.	Clark & Dickson 1971
Ph. clavum	4*	*Crematogaster* sp.	Clark & Dickson 1971
Aloeides thyra	4(*)^T	*Acantholepis capensis*	Claassens & Dickson 1980
A. dentatis	4^T	*Acantholepis capensis*	Henning 1983b
A. rossouwi	4(**)	*Acantholepis* sp.	Henning & Henning 1982
Erikssonia acraeina	4**	*Acantholepis* sp.	Henning 1984
Poecilmitis lycegenes	4**	*Crematogaster liengmei*	Henning 1983a
P. aureus	4**	*Crematogaster* sp.	Henning 1983a
P. chrysaor	4**	*Crematogaster liengmei*	Dickson 1943
P. felthami	4**	*Crematogaster* sp.	Clark & Dickson 1971
P. pyroeis	4**	*Camponotus (Tanaemyrmes) dicksoni*	Clark & Dickson 1971
P. palmus	3/4**	*Crematogaster peringueyi*	Claassens & Dickson 1980
P. thysbe	4**	*Crematogaster peringueyi*	Clark & Dickson 1971
P. brooksi	4**	*Crematogaster peringueyi*	Henning 1983a
P. perseus	4(**)	*Crematogaster* sp.	Ackery & Rajan 1990
P. nigricans	4**	*Crematogaster* sp.	Claassens & Dickson 1980
P. lysander	(4)**	*Crematogaster* sp.? (pupa)	Clark & Dickson 1971
P. kaplani	(4**)	*Crematogaster* sp.	Henning 1979
Oxychaeta dicksoni	4(*?)^T	*Crematogaster peringueyi*	Clark & Dickson 1971
Lycaenini:			
Lycaena heteronea	2	*Formica pilicornis*	Ballmer & Pratt 1988
L. rubidus	2	*Formica altipetens*	Funk 1975
L. xanthoides	2	*Formica pilicornis*	Ballmer & Pratt 1988
L. editha	2	*Formica altipetens*	Ballmer & Pratt 1988
L. dispar	1	*Myrmica rubra*	Hinton 1951
Theclini:			
Lucia limbaria	3/4(**)	*Iridomyrmex (gracilis* gr.)	Common & Waterhouse 1981
Paralucia aurifera	4**	*Iridomyrmex ?nitidiceps*	Common & Waterhouse 1981
P. spinifera	4**	*Iridomyrmex* sp.	Braby 1990
P. pyrodiscus	4**	*Notoncus enormis* *N. ectatommoides*	Braby 1990
Pseudodipsas eone	3(**)	*Iridomyrmex gilberti*	Common & Waterhouse 1981
Ps. cephenes	3(**)	*Iridomyrmex gilberti*	Common & Waterhouse 1981
Acrodipsas cuprea	4(*)	*Iridomyrmex* sp. *Crematogaster* sp.	Common & Waterhouse 1981 Cottrell 1984
A. myrmecophila	4*	*Iridomyrmex (nitidus* gr.)	
A. illidgei	4*	*Crematogaster (laeviceps* gr.)	Samson 1989
Hypochrysops apollo	4(**)	*Iridomyrmex cordatus* *Pheidole megacephala* (indiff.)	Common & Waterhouse 1981
H. arronica	4(**)	*Iridomyrmex scrutator*	Sands 1986
H. plotinus	4(**)	*Iridomyrmec cordatus*	Sands 1986
H. architas	3(**)	*Iridomyrmex cordatus*	Sands 1986
H. halyaetus	3(**)	*Crematogaster* sp.	Common & Waterhouse 1981
H. cyane	3/4(**)	*Iridomyrmex itinerans*	Common & Waterhouse 1981

Table 19 *(continued)*

Lycaenid species	Degree of myrmecophily	Associated ants	Reference(s)
Hypochrysops epicurus	3/4(**)	*Iridomyrmex ?nitidiceps*	Common & Waterhouse 1981
H. delicia	3/4(**)	*Crematogaster* sp.	Common & Waterhouse 1981
H. ignitus	4**	*Iridomyrmex* (*nitidus* gr.)	Common & Waterhouse 1981
H. piceatus	3(**)	*Iridomyrmex* (*itinerans* gr.)	Common & Waterhouse 1981
H. miskini	4(**)	*Iridomyrmex gilberti*	Common & Waterhouse 1981
H. digglesii	3(**)	*Crematogaster* sp.	Common & Waterhouse 1981
H. apelles	4**	*Crematogaster* sp.	Common & Waterhouse 1981
H. dicomas	4(**)	*Iridomyrmex* sp. (ov.)	Sands 1986
H. polycletus	4?(**)	*Iridomyrmex* sp. (ov.)	Sands 1986
H. theon	3/4(**)	*Iridomyrmex cordatus*	Common & Waterhouse 1981
Ogyris genoveva	4**	*Camponotus nigriceps*	Common & Waterhouse 1981,
		C. (*consobrinus* gr.)	Pierce & Elgar 1985
		C. perthianus	
		Iridomyrmex purpureus (attacked: Samson & O'Brien 1980)	
O. zosine	3**	*Camponotus claripes*	Hinton 1951,
		Oecophylla smaragdina	Common & Waterhouse 1981
O. idmo	3/4(**)	*Camponotus nigriceps*	Common & Waterhouse 1981
O. otanes	4**	*Camponotus* (*Myrmophyma*)	
		ferruginipes	Common & Waterhouse 1981
O. abrota	3(**)	*Crematogaster* sp.	Common & Waterhouse 1981
		Froggatella kirbyi	
		Technomyrmex ?albipes	
O. olane	2(**)	*Crematogaster* sp.	Common & Waterhouse 1981
O. ianthis	3(**)	*Froggatella kirbyi*	Common & Waterhouse 1981
O. iphis	3(**)	*Froggatella kirbyi*	Common & Waterhouse 1981
O. aenone	3(**)	*Pheidole* sp.	Common & Waterhouse 1981
		Iridomyrmex (*itinerans* gr.)	
O. amaryllis	3/4**	*Iridomyrmex* (*nitidiceps* gr.)	Common & Waterhouse 1981,
		I. (*rufoniger* gr.)	Aston & Dunn 1985
		Camponotus sp.	
		Crematogaster sp.	
Zesius chrysomallus	4*(*)	*Oecophylla smaragdina*	Hinton 1951
Jalmenus evagoras	4**	*Iridomyrmex anceps*	Pierce 1989
		I. (*rufoniger* gr.)	
J. eichhorni	3**	*Iridomyrmex* sp.	Common & Waterhouse 1981
J. ictinus	4**	*Iridomyrmex purpureus*	Pierce 1989
J. pseudictinus	4**	*Froggatella kirbyi*	Pierce 1989
J. daemeli	4**	*Iridomyrmex* (*rufoniger* gr.)	Pierce 1989
J. inous	3**	*Iridomyrmex ?gracilis*	Common & Waterhouse 1981
J. icilius	3/4**	*Iridomyrmex* (*rufoniger* gr.)	Common & Waterhouse 1981
J. clementi	2/3**	*Iridomyrmex* sp.	Common & Waterhouse 1981
Pseudalmenus chlorinda	3/4**	*Iridomyrmex foetans*	Common & Waterhouse 1981
Arhopala amphimuta	3/4**	*Crematogaster borneensis*	Maschwitz et al. 1984
A. moolaiana	3/4**	*Crematogaster borneensis*	Maschwitz et al. 1984
A. zylda	3/4**	*Crematogaster borneensis*	Maschwitz et al. 1984
A. amantes	4?(**)	*Oecophylla smaragdina*	Bell 1915
A. pseudocentaurus	4**	*Oecophylla smaragdina*	Kirton & Kirton 1987
A. centaurus	4**	*Oecophylla smaragdina*	Common & Waterhouse 1981

Table 19 *(continued)*

Lycaenid species	Degree of myrmecophily	Associated ants	Reference(s)
Arhopala micale	3**	*Oecophylla smaragdina*	Common & Waterhouse 1981
Thaduka multicaudata	2/3**	*Crematogaster* sp.	Hinton 1951
Flos fulgida	3**	*Hypoclinea* sp.	Ballmer & Pratt in press
Surendra vivarna	3**	*Anoplolepis longipes*	Maschwitz et al. 1985b
Thecla betulae	1/3	*Lasius niger* (pupae)	Emmet & Heath 1990
Shirozua jonasi	4	*Lasius spathepus*	Pierce & Elgar 1985
Quercusia quercus	0/2	*Lasius* sp.? (pupae)	Emmet & Heath 1990
Eumaeini:			
Catapaecilma elegans	3**	*Crematogaster* sp.	Hinton 1951
Myrina silenus	3**	*Camponotus* sp.	Henning 1983a
M. subornata	(2)**	*Pheidole rotundata* (lab)	Hinton 1951
Loxura atymnus	3**	*Oecophylla smaragdina* *Anoplolepis longipes* (ov.)	Hinton 1951, Maschwitz & Fiedler, pers. obs.
Eooxylides tharis	3**	*Anoplolepis longipes*	Maschwitz & Fiedler, pers. obs.
Drupadia theda	3**	*Crematogaster difformis*	Maschwitz et al. 1985b
D. ravindra	3**	*Tetramorium* sp.	Maschwitz & Fiedler, pers. obs.
Iolaus (Iolaphilus) alcibiades	0/2?	*Crematogaster buchneri* ?	Hinton 1951
I. (I.) julus	2*	*Crematogaster buchneri*	Hinton 1951
I. (Epamera) maesa	3(**)	*Crematogaster buchneri*	Farquharson 1922
Remelana jangala	3*	*Polyrhachis dives*	Young 1991
Hypolycaena erylus	4*	*Oecophylla smaragdina*	Jacobson 1912
H. phorbas	4*	*Oecophylla smaragdina*	Common & Waterhouse 1981
H. philippus	3*	*Camponotus acvapimensis* *C. maculatus* *Pheidole rotundata*	Hinton 1951
H. nigra	3(*)	*Pheidole aurivillii*	Hinton 1951
H. lebona	3*(*)	*Pheidole aurivillii*	Hinton 1951
Deudorix dinochares	2/3*(*)	*Pheidole* sp.	Ackery & Rajan 1990
D. ecaudata	3(*)	*Pheidole* sp.	Sevastopulo 1975
D. suk	3(*)	*Pheidole* sp.	Sevastopulo 1975
D. obscura	3(*)	*Crematogaster buchneri*	Hinton 1951
Rapala pheretima	3(**)	*Oecophylla smaragdina*	Norman 1976
R. iarbus	3**	*Anoplolepis longipes*	Fiedler, pers. obs.
R. manea	3**	*Crematogaster* sp.	Hinton 1951
Tomares ballus	2**	*Plagiolepis pygmaea*	Chapman & Buxton 1919
Arawacus lincoides [as *aetolus*]	3*	*Ectatomma tuberculatum* *E. ruidum*	Robbins & Aiello 1982, Robbins, in press
Rekoa palegon	3*	*Azteca* sp.	DeVries, pers. comm.

Table 19 *(continued)*

Lycaenid species	Degree of myrmecophily	Associated ants	Reference(s)
Harkenclenus titus	2*	*Formica subsericea*	Harvey & Webb 1980
		Camponotus nearcticus	
Satyrium edwardsii	3*	*Formica integra*	Webster & Nielsen 1983
S. ilicis	2*	*Camponotus aethiops*	Malicky 1969b, SBN 1987
S. esculi	3*	*Camponotus cruentatus*	Martín & Gurrea 1983
S. fuliginosum	3*	*Formica* (*rufa* gr.)	Ballmer & Pratt 1988
Panthiades bitias	3(*)	*Camponotus* sp.	Callaghan 1982
Tmolus echion	3*	*Ectatomma* sp. (ov.)	Robbins & Aiello 1982
Polyommatini:			
Candalides margarita	2**	*Technomyrmex sophiae*	Common & Waterhouse 1981
C. heathi	2**	*Iridomyrmex* (*gracilis* gr.)	Common & Waterhouse 1981
C. (Adaluma) urumelia	3**	*Monomorium* sp.	Edwards 1980
		(no larvae on plants with *Oecophylla smaragdina*)	
Anthene emolus	4**	*Oecophylla smaragdina*	Fiedler & Maschwitz 1989
A. seltuttus	4**	*Oecophylla smaragdina*	Common & Waterhouse 1981
A. lycaenina	2/3**	*Oecophylla smaragdina*	Hinton 1951
		Camponotus sp.	
A. lycaenoides	4**	*Oecophylla smaragdina*	Common & Waterhouse 1981
A. definita	2**	*Iridomyrmex* sp.	Claassens & Dickson 1980
A. pitmani	3**	*Crematogaster gerstaeckeri*	Jackson 1937
A. lunulata	3**	*Pheidole* sp.	Farquharson 1922,
		Technomyrmex detorquens	Jackson 1937
		Camponotus acvapimensis	
A. amarah	3**	*Crematogaster bequaerti*	Jackson 1937,
		Pheidole sp.	Milton 1990
		Myrmicaria sp.	
		Acantholepis affinis	
A. larydas	3**	*Crematogaster striatula*	Hinton 1951
		Pheidole aurivillii	
		Camponotus acvapimensis	
A. otacilia	3**	*Crematogaster* sp.	van Someren 1974
A. hodsoni	3(**)	*Pheidole* sp.	van Someren 1974
A. levis	4**	*Crematogaster* sp.	Ackery & Rajan 1990
A. sylvanus	3**	*Pheidole* sp.	Ackery & Rajan 1990
		Camponotus sp.	
A. lachares	3**	*Pheidole aurivillii*	Hinton 1951
		Ph. rotundata	
A. flavomaculatus	3*(*)	*Odontomachus haematodes*	Hinton 1951
		Crematogaster buchneri	
		Pheidole rotundata (lab)	
A. ? alberta	3(**)	*Crematogaster* sp.	Ackery & Rajan 1990
Triclema lucretilis	3(*)	*Crematogaster buchneri*	Hinton 1951
T. nigeriae	4**	*Crematogaster bequaerti*	Jackson 1937
		Pheidole rotundata (lab)	
Neurypexina lyzianus	3(**)	*Pheidole* sp.	Ackery & Rajan 1990
Niphanda fusca	4**	*Camponotus japonicus*	Iwase 1953

Table 19 *(continued)*

Lycaenid species	Degree of myrmecophily	Associated ants	Reference(s)
Nacaduba berenice	3**	*Solenopsis ?geminata* (lab)	Bean 1988
N. pactolus	2**	*Camponotus compressus*	Bean 1964, 1988
		Prenolepis sp.: indiff. (lab)	
		Crematogaster sp.: weakly attracted (lab)	
Prosotas dubiosa	2/3**	*Anoplolepis longipes*	Cassidy 1990
Theclinesthes onycha	2/3**	*Iridomyrmex glaber*	Common & Waterhouse 1981
		Notoncus ectatommoides	
		Paratrechina ?bourbonica	
		Polyrhachis (*ammon* gr.)	
Th. miskini	3**	*Oecophylla smaragdina*	Sibatani & Grund 1978,
		Crematogaster sp.	Common & Waterhouse 1981
Th. albocincta	3**	*Rhytidoponera metallica*	Grund & Sibatani 1975
		Iridomyrmex sp.	
		Camponotus sp.	
		Notoncus ?gilberti	
		Polyrhachis (*Campomyrma*) sp.	
Jamides bochus	2**	*Technomyrmex albipes*	Matsuoka 1976
J. celeno	2**	*Camponotus variegatus*	Corbet & Pendlebury 1978
Lampides boeticus	2**	*Camponotus compressus*	Hinton 1951,
		C. cruentatus	Claassens & Dickson 1980,
		C. sylvaticus	Martín Cano 1984, Schroth &
		C. foreli	Wiemers, pers. comm.
		Prenolepis clandestina	
		Lasius sp.	
		Acantholepis capensis	
		Plagiolepis sp.	
		Tapinoma melanocephalum	
		Iridomyrmex sp. (*humilis?*)	
		Dolichoderus bituberculatus (indiff.)	
Leptotes plinius	2/3**	*Crematogaster* sp.	Bell 1915
L. marina	3**	*Iridomyrmex humilis*	Ballmer & Pratt 1988
L. cassius	3**	*Crematogaster ashmeadi*	Downey & Allyn 1979
		Pheidole anastasii	
		Brachymyrmex heeri	
		Paratrechina bourbonica	
Castalius rosimon	2**	*Prenolepis* sp.	Hinton 1951
Tarucus ananda	3/4**	*Crematogaster* sp.	Bell 1915, Hinton 1951
T. waterstradti	3/4**	*Crematogaster* sp.	Maschwitz et al. 1985b
T. callinara	3(**)	*Crematogaster* sp.	Elfferich, pers. comm.
T. nara	3/4**	*Crematogaster* sp.	Bell 1915, Sevastopulo 1941,
		Pheidole latinoda	Hinton 1951
		Camponotus compressus	
T. rosaceus	3**	*Monomorium salomonis*	Chapman & Buxton 1919,
		Plagiolepis pygmaea	Rojo de la Paz,
		Camponotus sicheli	pers. comm.
T. thespis	3**	*Iridomyrmex humilis*	Claassens & Dickson 1980
Zintha hintza	2/3**	*Crematogaster jeanneli*	Jackson 1937
		Technomyrmex detorquens	

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Table 19 *(continued)*

Lycaenid species	Degree of myrmecophily	Associated ants	Reference(s)
Zizeeria karsandra	2/3**	*Tapinoma melanocephalum*	Corbet & Pendlebury 1978
Z. knysna	3**	*Tapinoma melanocephalum*	Warnecke 1932/33,
		Lasius niger (lab)	Elfferich, pers. comm.
Z. maha	3**	*Pheidole* sp.	Hinton 1951
Brephidium exilis	3**	*Conomyrma insana*	Fernández Haeger 1988
B. isophthalma	3**	*Tapinoma sessile*	Harvey & Longino 1989
Everes amyntula	2**	*Formica obscuripes*	Ballmer & Pratt 1988
		F. (*fusca* gr.)	
Cupido minimus	2*	*Lasius alienus*	Malicky 1969b, Baylis
		L. niger	& Kitching 1988,
		Formica fusca	Fiedler, pers. observ.
		F. rufibarbis	
		Plagiolepis vindobonensis	
		Myrmica rubra	
C. lorquinii	3*	*Tapinoma nigerrimum*	Munguira & Martín 1989,
		Plagiolepis pygmaea	Munguira, pers. comm.
C. osiris	3**	*Lasius alienus*	Malicky 1969b, SBN 1987
Pithecops fulgens	3*(*)	*Camponotus* (*Myrmanblys*) sp.	Ejima et al. 1978
		C. japonicus ?	
		Paratrechina flavipes ?	
Azanus ubaldus	3**	*Camponotus* sp.	Hinton 1951
		Prenolepis sp.	
A. natalensis	3**	*Cataulacus donisthorpei*	Hinton 1951
		Engramma ilgi	
Celastrina argiolus	2**	*Myrmica* sp.	Malicky 1969b, Harvey &
		Crematogaster lineolatus	Webb 1980, Kitching
		Camponotus japonicus	& Luke 1985, Emmet &
		C. nearcticus	Heath 1990
		Formica subsericea	
		F. truncorum	
		Lasius niger	
		L. alienus	
		L. fuliginosus	
Glaucopsyche lygdamus	3**	*Myrmica brevinodis*	Tilden 1947,
		Tapinoma sessile	Harvey & Webb 1980,
		Formica obscuripes	Pierce & Mead 1981,
		F. lasioides	Ballmer & Pratt in press
		F. subsericea	
		F. fusca	
		F. altipetens	
		F. puberula	
		F. comptula	
		F. neoclara	
G. piasus	3**	*Tapinoma sessile*	Newcomer 1912,
		Conomyrma sp.	Ballmer & Pratt 1988
		Prenolepis imparis	
		Formica pilicornis	

Table **19** *(continued)*

Lycaenid species	Degree of myrmecophily	Associated ants	Reference(s)
Glaucopsyche alexis	3**	*Myrmica scabrinodis*	Kontuniemi 1945,
		Crematogaster auberti	Malicky 1969b,
		Tapinoma erraticum	Martín Cano 1981, SBN 1987
		Formica cinerea	
		F. pratensis	
		F. nemoralis	
		F. fusca	
		F. subrufa	
		Camponotus aethiops	
		C. maxiliensis	
		Lasius alienus	
G. melanops	3**	*Camponotus foreli*	Malicky 1969b,
		C. cruentatus	Martín Cano 1981
		C. micans	
		C. sylvaticus	
Maculinea arion	4*	*Myrmica sabuleti*	Thomas et. al. 1989
		M. scabrinodis	
M. arionides	4(*)	*Myrmica* sp.	Iwase 1953
M. teleius	4*	*Myrmica scabrinodis*	Thomas et al. 1989
		M. rubra	
		M. vandeli	
		M. sabuleti	
M. nausithous	4*	*Myrmica rubra*	Thomas et al. 1989
		M. scabrinodis	
M. alcon	4*	*Myrmica ruginodis*	Thomas et al. 1989
		M. rubra	
		M. scabrinodis	Liebig 1989 (lab.)
M. rebeli	4*	*Myrmica schencki*	Thomas et al. 1989,
		M. sabuleti	Jutzeler 1989b
		M. scabrinodis	
		M. sulcinodis	
Iolana iolas	2*	*Tapinoma erraticum*	Warnecke 1932/33,
Pseudophilotes baton	2**	*Myrmica scabrinodis*	Malicky 1969b, Blab &
		Lasius alienus	Kudrna 1982
Euphilotes enoptes	3**	*Crematogaster mormonum*	Opler 1968, Shields 1973,
		Tapinoma sessile	Ballmer & Pratt in press
		Iridomyrmex humilis?	
		Formica neogagates	
Eu. rita	3**	*Dorymyrmex pyramicus*	Shields 1973,
		Camponotus nearcticus	Ballmer & Pratt in press
		C. essigi	
		Myrmecocystus kennedyi	
Eu. battoides	3**	*Tapinoma sessile*	Shields 1973,
		Iridomyrmex humilis	Ballmer & Pratt in press
		Formica (fusca-gr.)	
		F. subsericea	
		Lasius pallitarsus	
Eu. bernardino	3**	*Iridomyrmex humilis*	Shields 1973
Philotes sonorensis	3**	*Crematogaster mormonum*	Shields 1973,
		Tapinoma sessile	Ballmer & Pratt in press
		Formica obtusipilosa	

Table 19 *(continued)*

Lycaenid species	Degree of myrmecophily	Associated ants	Reference(s)
Scolitantides orion	3**	*Tapinoma erraticum* *Camponotus aethiops* *C. ligniperda* *C. vagus*	Malicky 1969b, Sanetra, pers. comm.
Euchrysops cnejus	3**	*Crematogaster* sp. *Iridomyrmex* sp. *Camponotus rubripes* *C. compressus* *Polyrhachis dives* *P. ammon*	Viehmeyer 1910a, Hinton 1951, Common & Waterhouse 1981
Eu. malathana	3**	*Monomorium* sp. *Pheidole rotundata* (lab) *Camponotus rubripes*	Farquharson 1922, Hinton 1951
Eu. dolorosa	2**	*Camponotus niveosetosus* (lab)	Henning 1983b
Eu. subdita crawshayinus	3**	*Monomorium minutum*	Jackson 1937
Lepidochrysops patricia	4*	*Camponotus maculatus*	Cottrell 1984
L. oreas	4*	*Camponotus niveosetosus*	Cottrell 1984
L. trimeni	4*	*Camponotus maculatus* *Plagiolepis* sp. ??	Henning 1983b
L. ignota	4*	*Camponotus niveosetosus*	Henning 1983b
L. quassi	4*	*Camponotus maculatus*	Farquharson 1922
L. variabilis	4*	*Camponotus niveosetosus*	Cottrell 1984
L. robertsoni	4*	*Camponotus niveosetosus*	Cottrell 1984
L. methymna	4*	*Camponotus maculatus*	Cottrell 1984
L. longifalces	4*	*Camponotus maculatus*	Cottrell 1984
Oboronia punctatus	4(*)	*Pheidole* sp.	Stempffer 1967
Chilades pandava	3**	*Monomorium speculare* *Crematogaster* sp. *Prenolepis longicornis*	Hinton 1951
Ch. lajus	2/3**	*Camponotus rubripes*	Hinton 1951
Ch. trochylus	3**	*Pheidole quadrispinosa* *Iridomyrmex* sp. *Prenolepis* sp.	Hinton 1951, Common & Waterhouse 1981
Ch. parrhasius	3**	*Camponotus sericeus*	Larsen 1984
Ch. galba	3(**)	*Monomorium gracillimum*	Parker 1983
Plebejus argus	3/4**	*Lasius niger* *L. alienus* *Formica cinerea* ??	Kitching & Luke 1985, C. Thomas 1985, Mendel & Parsons 1987, Jutzeler 1989e, Ravenscroft 1990
P. (Plebejides) martini	3**	*Crematogaster* sp.	Rojo de la Paz, pers. comm.
P. (P.) hespericus	3**	*Crematogaster auberti* *Formica subrufa* *F. cinerea* *Plagiolepis pygmaea* *P. schmitzi* *Camponotus cruentatus* *C. foreli* *C. sylvaticus*	Munguira & Martín 1989a, Munguira, pers. comm.

Table 19 *(continued)*

Lycaenid species	Degree of myrmecophily	Associated ants	Reference(s)
Pleb. (Plebejides) trappi	3**	*Formica lugubris*	SBN 1987, Schurian &
		F. lemani	Jutzeler, pers. comm.
P. (P.) sephirus	3**	*Tetramorium (caespitum* gr.)	Bálint & Kertész 1990,
		Formica pratensis	own observ.
		Camponotus aethiops	
		Lasius (alienus gr.)	
P. (Lycaeides) idas	3/4**	*Formica cinerea*	Malicky 1961 & 1969b,
		F. selysi	SBN 1987,
		F. exsecta	Jutzeler 1989d & 1990b
		F. lemani	
		F. pressilabris	
		F. lugubris	
		F. fusca ?	
		F. rufa & *F. nigricans*: attack	
P. (L.) melissa	3**	*Formica neogagates*	Ballmer & Pratt 1988
P. (L.) argyrognomon	3**	*Myrmica scabrinodis*	Malicky 1969b, Blab &
		M. sabuleti	Kudrna 1982
		Lasius alienus	
		L. niger	
P. (Icaricia) icarioides	3**	*Tapinoma sessile*	Downey 1962
		Formica integra	
		F. neogagates	
		F. fusca	
		F. integroides	
		F. oreas comptula	
		F. perspilosa	
		F. lasioides	
		Lasius neoniger	
		Dorymyrmex pyramicus	
		Solenopsis molesta ??	
P. (I.) acmon	3**	*Crematogaster coarctata*	Opler 1968, Ballmer
		Iridomyrmex humilis	& Pratt in press
		Formica pilicornis	
P. (I.) lupini	3**	*Formica pilicornis*	Ballmer & Pratt 1988
P. (I.) shasta	3**	*Formica fusca*	Emmel & Shields 1980,
		F. neogagtes	Ballmer & Pratt 1988
		F. oreas	
		F. densiventris	
P. (Plebulina) emigdionis	3**	*Formica pilicornis*	Ballmer & Pratt 1988
Polyommatus (Aricia) agestis	3**	*Myrmica sabuleti*	Jarvis 1958/59, Kitching
		Lasius alienus	& Luke 1985, Emmet & Heath
		L. flavus	1990, Schurian, pers. comm.
P. (A.) artaxerxes	3**	*Lasius* sp.	Malicky 1969b, SBN 1987
P. (A.) morronensis	3**	*Crematogaster auberti*	Munguira & Martín 1988
		Tapinoma erraticum	
		T. nigerrimum	
		Lasius niger	
P. (A.) eumedon	3**	*Myrmica* sp.	Malicky 1969b, Weidemann
			1986, SBN 1987

Table **19** *(continued)*

Lycaenid species	Degree of myrmecophily	Associated ants	Reference(s)
Polyommatus (Agrodiaetus) damon	3**	*Lasius niger*	Warnecke 1932/33, SBN 1987
		Formica pratensis	Malicky 1969b
P. (A.) thersites	3**	*Myrmica scabrinodis*	Rehfous 1954,
		Tapinoma erraticum	Malicky 1969b,
		Lasius alienus	Schurian, pers. comm.
P. (A.) semiargus	3**	*Lasius* sp.	Weidemann 1986
P. (Lysandra) coridon	3**	*Myrmica scabrinodis*	Malicky 1969b, Kitching
		M. sabuleti	& Luke 1985, Fiedler 1987b,
		M. schencki	Fiedler & Rosciszewski 1990
		Tetramorium caespitum	
		Lasius niger	
		L. alienus	
		L. flavus	
		L. fuliginosus ??	
		Plagiolepis vindobonensis	
		Formica rufa	
P. (L.) hispana	3**	*Crematogaster sordidula*	Maschwitz et al. 1975,
		Plagiolepis pygmaea	Schurian, pers. comm.
P. (L.) bellargus	3**	*Myrmica sabuleti*	Warnecke 1932/33,
		M. scabrinodis	Malicky 1969b, Blab &
		Tapinoma erraticum	Kudrna 1982, Kitching &
		Lasius alienus	Luke 1985, Jutzeler 1989c
		L. niger	
		L. flavus	
		Plagiolepis pygmaea	
P. (L.) punctifera	3**	*Monomorium salomonis*	Schurian & Thomas 1985
		Crematogaster scutellaris	
P. (L.) amandus	3**	*Lasius niger*	Hornemann, pers. comm.
P. (L.) escheri	3**	*Myrmica specioides*	SBN 1987, Fiedler, pers. obs.
		Formica cinerea	
P. (L.) dorylas	3**	*Myrmica scabrinodis*	Rehfous 1954, Weidemann
		Lasius alienus	1986, SBN 1987
		Formica cinerea	
P. (L.) golgus	3**	*Tapinoma nigerrimum*	Munguira & Martín 1989b
P. (L.) nivescens	3**	*Tapinoma nigerrimum*	Munguira & Martín 1989b
P. (Meleageria) daphnis	3**	*Tapinoma erraticum*	Schurian, pers. comm.,
		Formica pratensis	Fiedler, pers. obs.
		Lasius alienus	
P. (Polyommatus) icarus	2/3**	*Myrmica sabuleti*	Malicky 1969b,
		Lasius alienus	Martín Cano 1984,
		L. niger	Kitching & Luke 1985,
		L. flavus (lab)	SBN 1987, Jutzeler 1989d,
		Formica subrufa	Emmet & Heath 1990
		F. cinerea ?	
		Plagiolepis pygmaea	
P. (P.) eros	2/3**	*Myrmica gallienii*	Jutzeler 1989a
		Formica lemani	
Hemiargus ceraunus	3**	*Forelius pruinosus*	Ballmer & Pratt in press

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Development and variation of the suspensorium of primitive Catfishes (Teleostei: Ostariophysi) and their phylogenetic relationships

by

G. ARRATIA

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CONTENTS

INTRODUCTION

Catfishes are represented by over 2000 species assigned to about 32 families, largely distributed throughout South America, Africa, and Asia. Catfishes have traditionally been considered to exemplify a generalized morphology despite the tremendous variability of some structures between groups (Regan 1911, Alexander 1965, Howes 1983a, 1985, Arratia 1987a, 1990a, b). Phylogenetic investigations of most siluroid families have not been attempted, probably because our knowledge of this geographically widespread and morphologically diverse group is poor.

Recently, during the study of the family Diplomystidae (Arratia 1987a), I was faced with the problem of the identification of the pterygoid bones in diplomystids. I found that in some young *Diplomystes camposensis* an additional bone is present between the hyomandibula, quadrate, and metapterygoid (Arratia 1987a: 54, 98, Fig. 25A). Diplomystidae lack the bones traditionally recognized as the ectopterygoid (or pterygoid), and entopterygoid (endopterygoid or mesopterygoid); and yet some specimens may have one or two small bones. However, these do not occupy the position of the ecto- and entopterygoids in other teleosts (Arratia 1987a: 25, 40, 54, 98, 99, Figs. 6, 16, 25 A—D; Arratia & Schultze 1991: Fig. 36). As a consequence of this particular problem in diplomystids, I decided to study ontogenetic series of other catfishes to check whether the currently recognized metapterygoid, ectopterygoid, and entopterygoid of catfishes are homologous within catfishes and homologous with those of other teleosts.

I present here a detailed study of the ontogeny of the palatoquadrate and associated dermal and tendon bone pterygoids, dorsal part of the hyoid arch (hyo-symplectic), and their morphological relationships in primitive catfishes that have a small, triangular simple quadrate such as diplomystids (Diplomystidae), *Ictalurus* (Ictaluridae), and *Nematogenys* (Nematogenyidae). Further, I will compare these ontogenies to those of primitive catfishes that have a complex shaped quadrate such as *Noturus* (Ictaluridae) and *Parapimelodus* ("Pimelodidae"). However, before we can examine these ontogenies I will consider the ontogenetic studies of the suspensorium of primitive ostariophysans. Homologization of bones will follow two criteria: 1) embryonic origin and ontogeny of the bones and 2) shape, position and relationship of bones following Remane (1952); then these results will be tested in a phylogenetic context following Wiley (1981) and Ax (1987) to determine homologous and non-homologous characters. My usage of homology and non-homology follows Ax (1987: 152): "Homologous features are features in two or more evolutionary species which go back to one and the same feature of a common stem species. They may have been taken over from the stem species unchanged or else with evolutionary transformation." "Non-homologous features in two or more evolutionary species are features which were not present in the common stem species; they were evolved independent to each other."

METHODS

General methodology

Most specimens were cleared and double stained by the author for both cartilage and bone, following the procedure described in Schultze & Arratia (1986) and Arratia & Schultze (in press). The length of the specimens refers to the standard length, both in the text and figure captions; and the measurement was taken before clearing and staining.

Figures were prepared by the author using a Wild M5A stereo-dissecting microscope equipped with polarized light and camera lucida. Young specimens were examined with high resolution Olympus and Leitz compound microscopes, equipped with phase contrast and polarized light. Figures showing the lateral view of the left suspensorium exactly portray the position of the bones in situ and in addition, the hyomandibula maintains its precise relationship with the neurocranium. The figures were prepared while the fish was freely submerged in glycerine. The hyaline cartilage, secondary cartilage, and chondroidal regions are each differentially represented in the figures. Dermal bones and tendon bones are identified by capital letters on the illustrations.

Cladistic methodology

One set of assumptions is evaluated in this work: whether the pterygoid elements found in siluroids are modified pterygoids homologous with those of other teleosts; or whether they are new formations, and therefore non-homologous with the pterygoids of other teleosts. According to Patterson (1982), Wiley (1981), and Ax (1987), character homology should be tested in a phylogenetic context, with accepted phylogenies. If one requires accepted phylogenies to test homology, then I face the problem that there is no single publication resolving the relationships of siluroid families (the most recent study showed a polytomy among catfishes above Diplomystidae [contra Mo 1991]). There are only contributions related to a few groups (e.g., main hierarchical levels of catfishes: Grande 1987; Auchenipteridae: Ferraris 1988, Curran 1989; Diplomystidae: Arratia 1987a; Ictaluridae: Lundberg 1982; Loricarioidei: Baskin 1973, Howes 1985, Schaefer 1987, Pinna 1989; Siluridae: Bornbusch 1989; Pimelodinae: Lundberg et al. 1991 a; Pseudopimelodinae and Rhamdiinae: Lundberg et al. 1991b; Bagridae: Mo 1991), or a few characters, e.g., the Weberian complex (Chardon 1968) or the caudal skeleton (Lundberg & Baskin 1969, Arratia 1982, 1983). Based on the results of this paper, I will present the relationships of some primitive and advanced siluroids, to test the hypothesis of relationships proposed by Grande (1987) for Siluriformes, Siluroidei, and Siluroidea.

The phylogenetic techniques used in these analyses follow Hennig (1966), Wiley (1981), and Ax (1987), and were conducted using the PAUP (Phylogenetic Analysis Using Parsimony) software (version 3.0) of David L. Swofford (1990). Character states optimization used DELTRAN.

The analyses deal with two Taxa Sets. Taxa Set I was selected for ostariophysans represented by taxa selected for their presumed primitive sister group arrangement sen-

su Fink & Fink (1981), and Taxa Set II for a combined outgroup that includes gymnotoids and characiforms plus several primitive siluroids belonging to different families.

Two sets of characters were employed to analyse the relationships of ostariophysans (Data Set I), and catfishes (Data Set II). Data Set I consists of 131 characters and a total of 137 apomorphic character states. Data Set II consists of 75 characters and 92 apomorphic character states. Strict consensus trees were used to summarize the topologies of equally parsimonious trees.

Character determination

All characters are equally weighted and considered to be simple and independent of one another (Kluge & Farris 1969). Characters and character states are defined below. Missing data are coded as "?" in the data sets run with PAUP. The character number is followed by the character state in parenthesis (e.g., 1[1] is character state 1 of character 1).

Outgroup comparison

Outgroup comparison following Maddison et al. (1984) is used to polarize characters and ontogeny to test homology. In the present study, the primitive state of characters in Data Set I is determined by comparison to several primitive clupeocephalans, osteoglossomorphs, and elopomorphs, following Fink & Fink (1981), and in Data Set II by comparison to the gymnotoids (first outgroup) and the characiforms (second outgroup).

MATERIALS EXAMINED

Hundreds of cleared and stained specimens of different sizes were studied, as well as a large number of dry skeletons and alcoholic specimens, and serial cross sections of three trichomycterid catfishes. Institutional acronyms for specimens follow Leviton et al. (1985); except for the following collections: AG: Private collection of Dr. Atila Gosztonyi, Chubut, Argentina. PC: Private collection of the author. PU: Peabody Museum of Natural History, Yale University, New Haven, Connecticut. SIO: Scripps Institute of Oceanography, University of California, La Jolla, U.S.A. Material examined is listed below. Species are listed alphabetically within each higher taxon. The abbreviation for cleared and stained material is 'cl & st'; for examined specimens is 'sp'; for dry skeletal specimens is 'dry skel'; and for alcoholic dissected specimens is 'dissect'.

Halecomorphi
Amia calva: KU 3883, 8sp, cl & st; KU 21607, 1sp, cl & st; KU 21338, 1sp, cl & st; KU 22215, 1sp, cl & st.

Elopomorpha
Albula vulpes: UCLA W 49-122, 9sp, cl & st; UCLA W 52-122, 5sp, cl & st.
Elops affinis: UCL ST 0-29, 4sp, cl & st.
Elops hawaiensis: CAS(SU) 35103, 1sp, dry skel; CAS(SU) 35105, 1sp, dry skel.

Elops saurus: ANSP 147401, 2sp, cl & st; KU 3053, 3sp, cl & st; TCWC 0503.1, 5sp, cl & st; UMMZ 189355, 4sp, dry skel; UNC 13093, 1sp, cl & st.

Osteoglossomorpha
Hiodon alosoides: KU 7619, 6sp, cl & st; KU 9618, 3sp, cl & st.
Osteoglossum sp.: KU 22650, 2 sp, cl & st.

Clupeomorpha
Brevoortia patronus: KU 15113, 5 sp, cl & st.
Clupea harengus: PC 25986, 14 sp, cl & st.
Coilia nasus: PC 020989, 9sp, cl & st.
Denticeps clupeoides: MNHN 1960-391, 2sp, cl & st; MRAC 73-32P-4915-932, 3sp, cl & st.
Dorosoma cepedianum: KU 21802, 36sp, cl & st.
Engraulis encrasicholus: KU 19941, 8sp, cl & st.
Engraulis ringens: PC 010689, 8sp, cl & st.
Jenkinsia lamproteica: KU uncat., 10sp, cl & st.

Esocoidei
Esox americanus: KU 6041, 4sp, cl & st; KU 17864, 4sp, cl & st.
Umbra limi: KU 10370, 6sp, cl & st.

Ostariophysi
Gonorynchiformes
Chanidae:
Chanos chanos: CAS-SU 35075, 1sp, dry skel; CAS-SU 38340, 2sp, cl & st; PC uncat., 1sp, dissect; SIO 80-199, 7sp, cl & st; UMMZ 196864, 1sp, cl & st.

Gonorynchidae:
Gonorynchus abbreviatus: CAS 30993, 1sp, cl & st.

Cypriniformes

Catostomidae:
Carpiodes carpio: KU 1996, 3sp, cl & st; KU 21807, 30sp, cl & st.

Cyprinidae:
Campostoma anomalum: KU 12092, 3sp, cl & st.
Clinostomus funduloides: KU 3262, 2sp, cl & st; KU 10697, 3sp, cl & st.
Ctenopharyngodon idella: KU 21614, 1sp, dry skel; KU 22100, 1sp, dry skel.
Cyprinella lutrensis: KU 12089, 2sp, cl & st; KU 15793, 6sp, cl & st;
Cyprinella xanthicara: ASU 3642, 9sp, cl & st.
Cyprinus carpio: KU 3790, 1sp, cl & st; KU 15336, 1sp, dry skel; KU 172321, sp, dry skel; KU 21377, 1 sp, dry skel.
Dionda episcopa: KU 7427, 5sp, cl & st.
Opsariichthys bidens: CAS-SU 32512, 2sp, cl & st; CAS-SU 68907, 2sp, cl & st; PC 22, 4sp, cl & st; PC 22, 2sp, dissect.
Zacco platypus: PC 21, 10sp, cl & st.

Characiformes
Characidae:
Astyanax sp.: KU 20099, 7sp, cl & st.
Brycon argenteus: KU 10543, 2sp, cl & st; KU 10543, 2sp, dissect; PC 218, 7sp, cl & st; PC 219, 30sp, cl & st.
Cheirodon pisciculus: PC 130173, 10sp, cl & st; PC 230173, 45 sp, cl & st.
Gymnocharacinus bergi: KU 19199, 1sp, cl & st.

Distichodontidae:
Xenocharax spilurus: CAS-SU 15639, 2sp, cl & st.

Erythrinidae:
Hoplias malabaricus: KU 13636, 2sp, cl & st; KU 13636, 2sp, dissect.

Siluriformes (sensu Fink & Fink 1981)
Siluroidei
Ariidae:
Galeichthys felis: KU 19590, 10sp, cl & st; KU 19590, 1sp, dissect.
Bagre marinus: KU 3053, 3sp, cl & st; KU 3053, 1 sp, dissect; KU 21380, 1sp, dry skel.

'Bagridae':
Mystus tengara: KU 12170, 1sp, cl & st.

Bunocephalidae:
Bunocephalus coragoideus: ANSP 139313, 1sp, cl & st.

Callichthyidae:
Callichthys callichthys: KU 13722, 3sp, cl & st; KU 13724, 2sp, cl & st.

Claridae:
Clarias sp.: PC 111189, 2sp, cl & st.
Uegitglanis zammazanoi: PC 120677, 1sp, cl & st.

Diplomystidae:
Diplomystes camposensis: KU 19210, 1sp, cl & st; PC 011086b, 3sp, cl & st; PC100487, 1sp, dissect; PC 110276, 2sp, cl & st; PC 130276, 1sp, cl & st; PC 140276, 1sp, cl & st; PC 220189, 2sp, dissect.
Diplomystes chilensis: CAS (SU) 13706, 2sp, dissect; MCZ 8290, 2sp, cl & st; MNHN B.585, 1sp, dissect.
Diplomystes nahuelbutaensis: BMNH 1876-10-2:22, 1sp, dry skel; CAS-SU 55425, 1sp, cl & st; MCZ 61245, 1sp, dissect; PC 230186, 3sp, cl & st.
Olivaichthys viedmensis: AG uncat., 1sp, cl & st; PC 20279, 1sp, cl & st; FMNH 58004, 3sp, cl & st; FMNH 58004, 3 sp, radiographs.

†Hypsidoridae:
Hypsidoris farsonensis: PU 20570a-b, 1sp.

Ictaluridae:
Ameiurus catus: KU 1741, 1, dry skel; KU 8332, 2sp, cl & st; KU 10151, 3sp, cl & st; KU 10151, 1sp, dissect.
Ameiurus melas: KU 15181, 2sp, cl & st; KU 1038, 1sp, cl & st; KU uncat., 2sp, dissect.
Ictalurus furcatus: KU 1747, 1sp, dry skel; KU 11343, 1sp, dry skel; KU 15866, 1sp, dry skel; KU 21381, 1sp, dry skel.
Ictalurus punctatus: KU 9657, 9sp, cl & st; KU 15340, 1sp, dry skel; KU 15342, 1sp, dry skel; KU uncat., 50sp, cl & st; KU uncat., 85sp, cl & st; KU 4162, 2sp, dissect.
Noturus exilis: KU 17229, 61sp, cl & st; KU 17229, 2 sp, dissect.
Noturus hildebrandi: KU uncat., 12sp, cl & st.
Pylodictis olivaris: KU 1746, 3sp, cl & st; KU 2386, 1sp, dry skel; KU 10414, 3sp, cl & st; KU 13122, 1sp, dry skel; KU 15697, 2sp, cl & st; KU 16830, 2sp, cl & st; KU 17970, 1sp, cl & st; KU uncat., 1sp, dissect.

Loricariidae:
Ancistrus hoplogenus: KU 13755, 1sp, cl & st.
Hypostomus plecostomus: KU 13948, 2sp, cl & st.
Hypostomus sp.: KU 21823, 3sp, cl & st.

Loricaria uracantha: KU 17710, 2sp, cl & st.

Loricarichthys sp.: ANSP 131612, 2sp, cl & st.

Nematogenyidae:

Nematogenys inermis: PC 131, 8sp, cl & st; PC 206, 3sp, cl & st; PC 208, 2sp, cl & st; PC 30873, 6sp, cl & st; PC 230390, 4sp, cl & st; PC 051188, 1sp, dissect; PC uncat., 1sp, dissect.

'Pimelodidae':

Heptapterus mustelinus: KU 21235, 4sp, cl & st; PC 147, 1sp, cl & st; PC 147, 1sp, dissect; PC 19484, 1sp, cl & st; PC 17583, 2sp, cl & st; PC 50983, 4sp, cl & st.

Microglanis variegatus: KU 20009, 10sp, cl & st.

Parapimelodus valenciennesi: KU 21804, 10sp, cl & st; ZMH 6669, 2sp, cl & st; PC uncat., 1sp, dissect.

Pimelodella hasemani: KU 13695, 1sp, cl & st.

Pimelodella sp.: KU 137010, 3sp, cl & st.

Pimelodus maculatus: PC 271282, 2sp, cl & st.

Pimelodus sp.: KU 21805, 2sp, cl & st; PC uncat., 2sp, dissect.

Rhamdia sapo: KU 21806, 3sp, cl & st; PC 100285, 2 sp, dissect.

Rhamdia wagneri: KU 20012, 3sp, cl & st.

Schilbeidae:

Ailia coilia: KU 12156, 1sp, cl & st.

Eutropiichthys vacha: KU 12169, 1sp, cl & st.

Schilbeidae ind.: KU uncat., 4sp, cl & st.

Trichomycteridae:

Bullockia maldonadoi: KU 19371, 20sp, cl & st; PC 210986, 20sp, cl & st.

Eremophilus mutisii: CAS-SU 62927, 2sp, cl & st.

Hatcheria macraei: KU 19247, 10sp, cl & st.

Ochmacanthus reinhardti: KU 13726, 1sp, cl & st; KU 13735, 2sp, cl & st.

Trichomycterus areolatus: KU 19423, 20sp, cl & st; KU 19424, 14sp, cl & st; KU 19425, 20sp, cl & st; PC 221081, 20sp, cl & st.

Trichomycterus chiltoni: KU 19227, 9sp, cl & st.

Trichomycterus roigi: PC 230281-2, 13sp, cl & st.

Trichomycterus rivulatus: KU 19181, 3sp, cl & st; KU 19360, 2sp, cl & st.

Tridentopsis pearsoni: CAS-SU 56200, 2sp, cl & st.

Vandellia cirrhosa: AMNH 20497, 1sp, cl & st; UMMZ 205178, 10 sp, cl & st.

Gymnotoidei

Gymnotidae:

Gymnotus carapo: KU 13793, 9sp, cl & st; KU 21803, 1sp, cl & st.

Gymnotus cylindricus: KU 1869, 2sp, cl & st.

Hypopomidae:

Hypopomus brevirostris: KU 13800, 7sp, cl & st.

Hypopygus lepturus: KU 20127, 1sp, cl & st.

For other specimens used in comparative studies see list of materials in Arratia (1990a) and Arratia & Schultze (1991).

TERMINOLOGY

The differentiation of a cartilaginous plate into separate, articulating elements (Arratia 1990a, Arratia & Schultze 1990) is characterized by structural changes that produce changes in the density of the cartilage in the area where an articulation will form. The articular region itself is characterized by a change in the position of the cartilage cells, so that it appears more or less dense and fibers develop. The appearance of the future articular region under a compound microscope or stereomicroscope shows differences among species. For instance, a clear, less dense region appears where an articulation will form in trichomycterids (Fig. 1), or a more dense region than the surrounding areas will
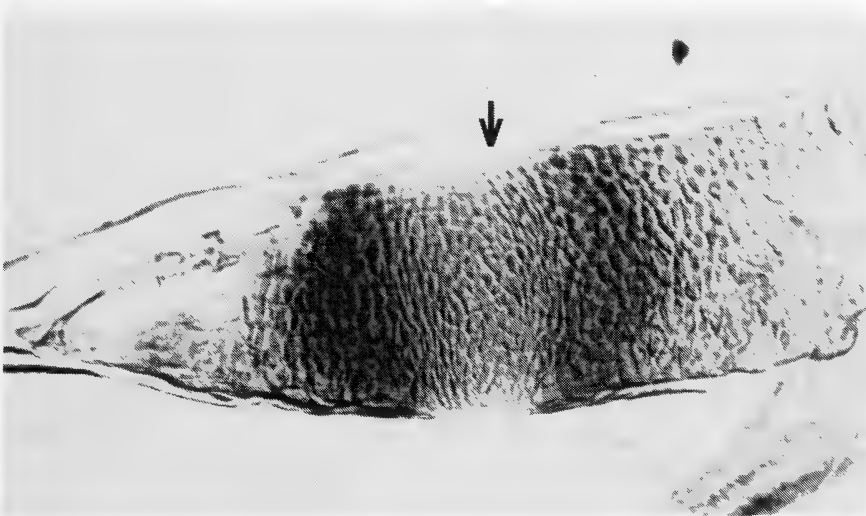
Fig.1: Pterygoquadrate portion of the hyo-symplectic-pterygoquadrate plate of *Trichomycterus areolatus* (22 mm specimen; PC 221081) illustrating the changes of the density of the cartilage where an articulation will form (indicated by an arrow) (after Arratia 1990a).
mtg: metapterygoid; q: quadrate.

form in ictalurids. Changes in density are due to different positions and distributions of the cartilaginous cells and fibers. Secondary cartilage and chondroid bone is usually found in the articular facets of synchondral articulations of large specimens, as already established by Beresford (1981) and Smith & Hall (1991).

The types of articulation between bones of the suspensorium differ among teleost groups. Sutures are described as serrate, dentate, harmonic, etc... following the terminology of human anatomy (Gray 1982), in the absence of a specific terminology for fishes. In the early ontogeny of teleosts, the surfaces producing a sutural joint are smooth (harmonic suture) and from this stage the suture may be modified into a dentate or serrate one, or stay as a harmonic suture (see below). Combinations of articulations are explained in the text.

I distinguish here: autopalatine from dermopalatine, true pterygoid bones (metapterygoid, ectopterygoid, and entopterygoid) sensu Arratia & Schultze (1991), rudimentary and/or sesamoid pterygoids ('entopterygoids'), and additional pterygoids (identified here as 1, 2, 3 . . . etc).

Autopalatine

The name palatin was used by Geoffroy St. Hilaire (1824) and Cuvier & Valenciennes (1828), palatinum by Hallmann (1837), and palatine by Owen (1843, 1846, 1866) and Parker & Bettany (1877) to identify the anterior styliform ossification of the palatoquadrate that bears teeth in the perch, salmon, and other teleosts. It corresponds to a compound element formed by autopalatine and dermopalatine according to modern literature. The name auto-palatine was used first by Allis (1898: 459, Pl. 33, fig. 2) in his description and illustration of *Amia calva*. Later, auto-palatine was changed to autopalatinum (e.g., Holmgren & Stensiö 1936) or autopalatine (e.g., Stensiö 1925, Jarvik 1942).

The term autopalatine is reserved here for the anteriormost ossification of the palatoquadrate, and the term dermopalatine for a dermal ossification which develops ventrolateral to pars autopalatina of the palatoquadrate and bears dentition. Siluroids have an autopalatine; the dermopalatine is absent (see below).

Pterygoid bones

Teleostean pterygoid bones generally consist of the following:

M e t a p t e r y g o i d : It is a chondral bone (Parker 1873, Gaupp 1905) which originates from the posterodorsal part of the cartilaginous palatoquadrate; it overlaps laterally the hyo-symplectic cartilage early in ontogeny (gymnotoids are an exception) (see Arratia & Schultze 1991 for details). The metapterygoid in adults may be sutured (serrate, dentate, or hamonic) and/or synchondrally articulated with the quadrate and hyomandibula posteriorly; it sutures anteriorly with the entopterygoid.

The metapterygoid was identified in teleosts as temporal by Cuvier & Valenciennes (1828), as pre-tympanic by Owen (1843, 1846), and as metapterygoid by Parker & Bettany (1877). Starks (1926) labelled the metapterygoid in siluroids as pterygoid; recently, Howes & Ayanomiya Fumihito (1991) identified the siluroid metapterygoid as the posterior pterygoid. The metapterygoid in siluroids is homologous with that in other fishes (see Allis 1923, Arratia & Schultze 1991), so that there is no reason to replace the name metapterygoid by another name in siluroids.

E n t o p t e r y g o i d : It is a dermal bone at the medial side of the palatoquadrate, between the autopalatine anteriorly and the metapterygoid posteriorly. It supports the eye in amiids and most teleosts (for details see Arratia & Schultze 1991).

The entopterygoid in teleosts was named ptérygoidien interne or pterygoideum internum by Cuvier & Valenciennes (1828) and Hallmann (1837), and entopterygoid by Owen (1843, 1846, 1866). Therefore, the name entopterygoid was used first to identify

the dermal medial pterygoid bone of the palate in actinopterygians (e.g., cypriniforms, characiforms, osteoglossomorphs, percomorphs, polypterids, lepisosteids). According to Owen (1866: Figs. 81, 98) the bone that he interpreted as entopterygoid in fishes and labelled as 23 in his figures does not have an homologous element in reptiles. Later on, the names entopterygoid or endopterygoid were used to identify the dermal medial bone of the palate in *Amia calva* by Goodrich (1930: Figs. 429, 430). Recently, Jollie (1962) used the name pterygoid to identify the medial dermal bone of the palate of fishes (e.g., salmonid: Fig. 5-1; *Lepisosteus*: Fig. 5-14E; *Amia*: Fig. 5-14F; *Eusthenopteron*: Fig. 4-31) and tetrapods (e.g., *Seymouria*: Fig. 4-26C; *Palaeogyrinus*: Fig. 4-24B; bullfrog: Fig. 4-21C). Nevertheless, it has not been demonstrated yet that the piscine entopterygoid and the tetrapod pterygoid are homologous; according to Lubosch (1907), van Kampen (1922), and de Beer (1929), the mammalian pterygoid is a composite structure.

For reasons I have not been able to find in the literature, the entopterygoid has been commonly identified as the mesopterygoid in siluroids and other ostariophysans (e.g., Regan 1911, Weitzman 1962, Fink & Fink 1981). The term mesopterygoid was created and used by Parker (1874, 1885, 1886) and Parker & Bettany (1877) for the dermal bone at the medial boundary of the palate in teleosts and tetrapods as well. (In *Galeopithecus*, Parker 1885 described and figured a bone he called mesopterygoid which exists in addition to the pterygoid, and which he also showed in the pig [1887].) Broom (1922) named mesopterygoid the region that corresponds to the pars metapterygoidea of the palatoquadrate in the sarcopterygian *Eusthenopteron* and Goodrich (1930: Fig. 407) identified the entopterygoid of *Salmo fario* as the mesopterygoid. Since the term mesopterygoid does not imply any special condition in ostariophysans and/or siluroids, I retain the term entopterygoid proposed first for teleosts.

E c t o p t e r y g o i d : It is a dermal bone at the lateral or ventrolateral portion of the palatoquadrate, posterior to pars autopalatina and anterior to pars quadrata of the palatoquadrate (for details see Arratia & Schultze 1991). The ectopterygoid extends anterodorsally beyond the dermopalatine and autopalatine in primitive teleosts (e.g., Arratia & Schultze 1991: Fig. 24), but barely contacts the autopalatine in most other teleosts. Commonly, it is considered to be absent in siluroids according to Alexander (1965), Gosline (1975), and herein.

The bone was identified as adgustal by Geoffroy St. Hilaire (1824), transverse by Cuvier & Valenciennes (1828) and Agassiz (1843), pterygoideum externum by Hallmann (1837), pterygoid by Owen (1843, 1846), Parker & Bettany (1877), Regan (1911), and others in teleosts. The name ectopterygoid was used first by Owen (1866: 157) for reptiles: the ectopterygoid in lizards forms the outer boundary of the pterygo-maxillary or palatine vacuity, whereas it forms the hind boundary in crocodiles. The reptilian ectopterygoid of Owen, labelled as bone 25 (Owen 1866: 133, Fig. 98) corresponds (his interpretation) to the piscine subdivision 25 (Owen 1866: Fig. 81 = actually recognized as hyomandibula). Therefore, the reptilian ectopterygoid (bone 25) is not homologous with the piscine bone 25 sensu Owen (1866) that is the hyomandibula in fishes. The bone that

actually is identified as the ectopterygoid in fishes, was named pterygoid by Owen (1843, 1846, 1866); however, pterygoid is the term that actually identifies the dermal medial pterygoid in tetrapods.

The name ectopterygoid in fishes was used first by Sagemehl (1885) in his osteological description of characiforms and since then it has been used for actinopterygians (e.g., Allis 1889, Pearson & Westoll 1979, Gardiner 1984) and sarcopterygians (e.g., Jarvik 1942, 1980). To my best knowledge the homology of the piscine ectopterygoid has never been addressed; for the purpose of the present paper, the name ectopterygoid will be used. I will deal in a separate paper with the homologization of the tetrapod and piscine ectopterygoids.

D e r m o + m e t a p t e r y g o i d : It is a compound bone formed by the ontogenetic fusion of the metapterygoid and a dermal tooth plate (e.g., *Parapimelodus*).

E c t o p t e r y g o i d + s u b p a l a t i n e t o o t h p l a t e : It is a dermal, toothed bone that occupies the position of both the ectopterygoid and dermopalatine in primitive teleosts (e.g., *Eutropiichthys*). This element corresponds to the ectopterygoid of Tilak (1961); tooth plate of Gosline (1975).

Sesamoid pterygoids

Pterygoids differing in number and shape occur within the siluroids. I recognize as sesamoid 'entopterygoids' and 'ectopterygoid' any small, otherwise unnamed bone that originates as a mineralization of a ligament (=tendon bone herein) and is connected to the cranium and/or palate by ligaments and connective tissue. For the purposes of this paper the tendon-bone and/or sesamoid entopterygoid and ectopterygoid will be distinguished as 'entopterygoid' and 'ectopterygoid'. Several types of 'entopterygoids' (Fig. 2A—G) may be named according to their position, shape, and ligamentous connections; number 1 corresponds to the type having the least number of ligamentous connections; numbers 2, 3, etc., indicate the addition or change of ligamentous connections.

' E n t o p t e r y g o i d ' t y p e 1 : (Mesopterygoid of Regan 1911, Alexander 1965.) Small, sesamoid, irregularly shaped bone, anteromedial to the processus basalis of the metapterygoid. The 'entopterygoid' type 1 is connected by ligaments (Fig. 2A) to the metapterygoid and to the vomer (occasionally present in Diplomystidae, e.g. *Olivaichthys viedmensis*).

' E n t o p t e r y g o i d ' t y p e 2 : (Endopterygoid of Arratia et al. 1978, 'entopterygoid' of Arratia 1990a.) Small sesamoid bone forming a cup-like ossification around the distal cartilage of the autopalatine. A strong, short ligament (Fig. 2B) extends between the 'entopterygoid' type 2 and the metapterygoid. A long ligament connects the 'entopterygoid' type 2 and the anterior part of the vomer. The 'entopterygoid' is closely attached to the autopalatine by connective tissue (e.g., *Nematogenys*).
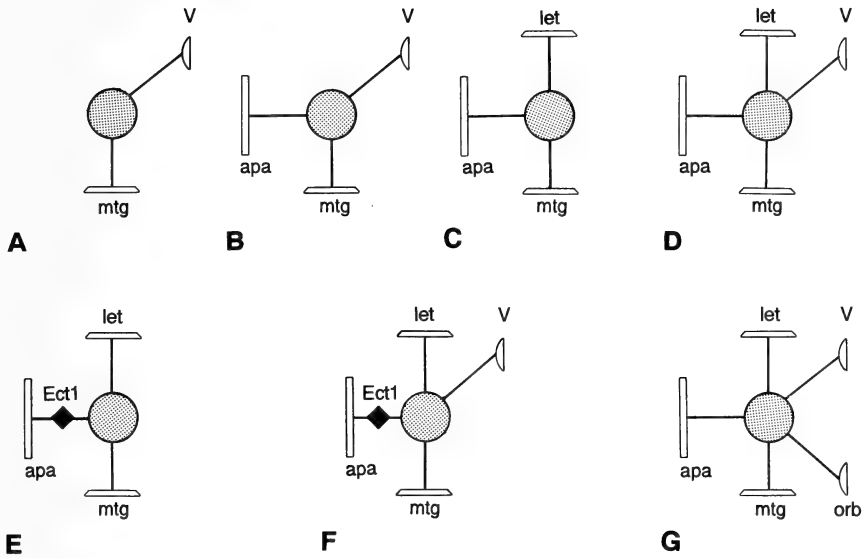
Fig.2: Diagram of the ligamentous connection of 'entopterygoid' types 1 to 7 to palatal and cranial bones in catfishes. The circle represents an 'entopterygoid'. — A: 'Entopterygoid' type 1; B: 'Entopterygoid' type 2; C: 'Entopterygoid' type 3; D: 'Entopterygoid' type 4; E: 'Entopterygoid' type 5; F: 'Entopterygoid' type 6; G: 'Entopterygoid' type 7.
apa: autopalatine; Ect 1: 'ectopterygoid' type 1; let: lateral ethmoid; mtg: metapterygoid; orb: orbitosphenoid; V: vomer.

'E n t o p t e r y g o i d' t y p e' 3: (Ectopterygoid of Tilak 1964.) Rudimentary splint-like, sesamoid bone between the two anterior sharp processes of the metapterygoid; metapterygoid and 'entopterygoid' are connected by a short ligament (Fig. 2C). The 'entopterygoid' type 3 is connected by connective tissue and ligaments to metapterygoid, autopalatine, and lateral ethmoid (e.g., *Eutropiichthys*).

'E n t o p t e r y g o i d' t y p e 4: Small, flat, slightly square sesamoid bone found anterior to the metapterygoid and medial to the autopalatine. This type of 'entopterygoid' is linked by ligaments (Fig. 2D) to the metapterygoid, vomer, autopalatine, and lateral ethmoid (e.g., *Heptapterus, Rhamdia*, and *Noturus*).

'E n t o p t e r y g o i d' t y p e 5: (Mesopterygoid of Regan 1911, Gosline 1975, ectopterygoid of Azpelicueta et al. 1981.) Small, thick, crescentic or triangular, sesamoid bone posterior to the 'ectopterygoid' type 1 (see below) and medial to the autopalatine. It is linked by connective tissue and ligaments (Fig. 2E) to the metapterygoid and lateral ethmoid, and by an indirect ligamentous link to the autopalatine through the 'ectopterygoid' type 1 (e.g., *Parapimelodus*).

'E n t o p t e r y g o i d' t y p e 6 : (Mesopterygoid of Jayaram 1966.) Small, flat, slightly triangular, sesamoid bone posterior to the 'ectopterygoid' type 1 and medial to the autopalatine. The 'entopterygoid' type 6 has connections (Fig. 2F) similar to those of 'entopterygoid' type 5, but there is an additional ligamentous link to the vomer (e.g., *Bagre marinus* and *Galeichthys*).

'E n t o p t e r y g o i d' t y p e 7 : (Endopterygoid of Lundberg 1982.) Small, triangular or square, sesamoid bone medial to the autopalatine and anterior to the metapterygoid. This type of 'entopterygoid' is attached by connective tissue and ligaments (Fig. 2G) to the autopalatine, metapterygoid, orbitosphenoid, lateral ethmoid, and anterior portion of the vomer (e.g., *Ictalurus*).

'E c t o p t e r y g o i d' t y p e 1 : (Pterygoid of Regan 1911, palatine element number 2 of Starks 1926, fractured mesopterygoid of Gosline 1975, ectopterygoid of Rao & Lakshmi 1984.) Elongate or cup-like bone ventrally attached to the autopalatine or articulating with the anterior portion of the autopalatine; it commonly extends posterior to the distal part of autopalatine. A short, strong ligament (Fig. 2E,F) extends between 'ectopterygoid' type 1 and 'entopterygoid' type 6 (e.g., *Bagre marinus* and *Galeichthys*), and between 'ectopterygoid' type 1 and 'entopterygoid' type 5 (e.g., *Parapimelodus, Pimelodus*).

Additional pterygoids

An additional pterygoid is considered here to be a dermal bone that differs in shape and position from the metapterygoid, ectopterygoid, 'entopterygoid' types 1 to 7, and 'ectopterygoid' type 1. It may be an additional bone to the pterygoid series.

P t e r y g o i d   t y p e   1 : Rudimentary, flat, elongate dermal bone between the posterodorsal part of the metapterygoid and the anterior membranous outgrowth of hyomandibula. It appears fused to the metapterygoid in a few specimens of *Parapimelodus*.

Origin and ossification of bones of suspensorium

In all fishes examined, as well as other osteichthyans (see Arratia & Schultze 1991), the bones of the suspensorium have a variety of origins:

    cartilaginous origin
        mandibular arch: autopalatine
                           metapterygoid
                           quadrate
        hyoid arch: hyomandibula
                           symplectic
    dermal origin   dermopalatine
                           tooth plates associated with palatal bones
                           ectopterygoid

entopterygoid

pterygoid type 1

tendon bone origin   'entopterygoid'

'ectopterygoid'

The bones which originate from cartilaginous arches exhibit chondral ossification, and those of dermal origin exhibit dermal ossification (that is, they do not include a cartilaginous precursor).

Ossification of the cartilaginous arches giving rise to the bones of the suspensorium begins at the surface, they therefore exhibit perichondral ossification. In addition, bones such as the hyomandibula, symplectic, metapterygoid, and quadrate may have membranous outgrowths associated with the chondral portion. These membranous outgrowths are not preformed in cartilage; they are thin, delicate ossifications that extend from the perichondral ossification.

SUSPENSORIUM OF OSTARIOPHYSANS OTHER THAN CATFISHES

Gonorynchiforms

The series of *Chanos chanos* includes 13 specimens ranging from 11 to about 850 mm standard length.

In 11—13.5 mm specimens, the mandibular and hyoid arches (Figs. 3, 4A) are cartilaginous. The dorsal part of the mandibular arch, the palatoquadrate, is an elongate cartilage that overlaps the lateral face of the dorsal limb of the hyoid arch. The palatoquadrate cartilage is continuous with the lower part of the mandibular arch, the Meckelian cartilage. The palatoquadrate broadens posteriorly and close to the
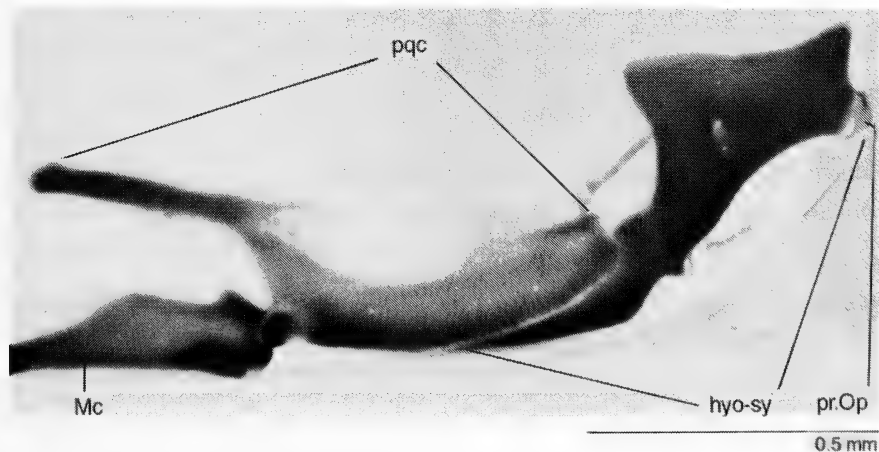
Fig.3: Suspensorium of the gonorynchiform *Chanos chanos*, lateral view (13.5 mm specimen; SIO 80-199). hyo-sy: hyo-symplectic; mc: Meckelian cartilage; pqc: palatoquadrate; pr. Op: processus opercularis.

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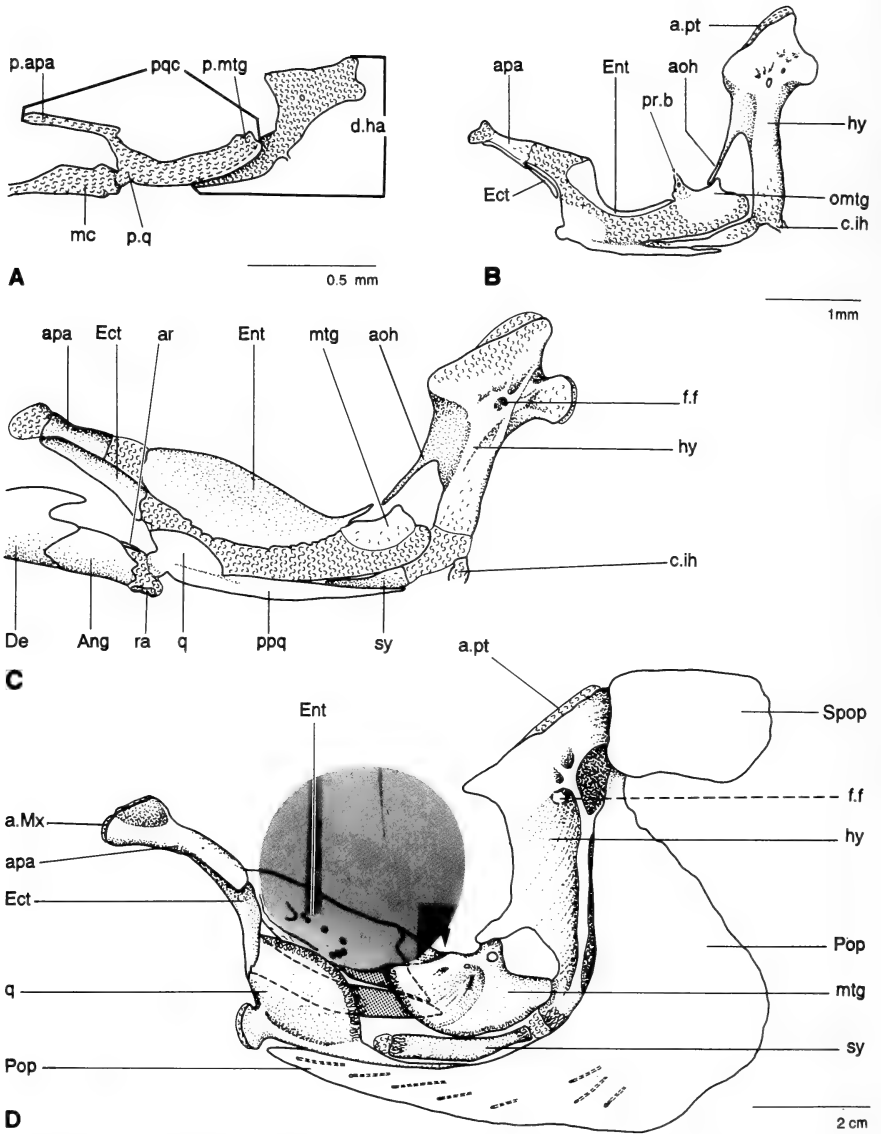
Fig.4: Suspensorium of the gonorynchiform *Chanos chanos*, lateral view and placement of the eye (dotted area). — A: 13 mm specimen (SIO 80-199); B: 16.5 mm specimen (SIO 80-199); C: 21 mm specimen (UMMZ 196864); D: 148 mm cranial length (CAS-SU 35075; after Arratia 1990a). Arrow points to a notch. Cartilage missing. Ang: angular; aoh: anterior outgrowth of hyomandibula; apa: autopalatine; a.Mx: articular facet for maxilla; a.pt: articular facet for pterotic; ar: articular; c.ih: cartilaginous interhyal; De: dentary; d.ha: dorsal limb of hyoid arch; Ect: ectopterygoid; Ent: entopterygoid; f.f: foramen for passage of hyoideomandibular nerve trunk; hy: hyomandibula; mc: Meckelian cartilage; mtg: metapterygoid; omtg: ossification center of metapterygoid; p.apa: pars autopalatina; p.mtg: pars metapterygoidea; Pop: preopercle; ppq: posteroventral process of quadrate; p.q: pars quadrata; pqc: palatoquadrate cartilage; q: quadrate; ra: retroarticular; Spop: suprapreopercle; sy: symplectic.

posterodorsal margin is the pars metapterygoidea which has a medial cartilaginous projection, the processus basalis. In a 13.5 mm specimen, the condylar region of the pars quadrata begins to increase in density and a fine perichondral ossification (of the quadrate) surrounds the condyle. A long, fine posteroventral process ossifies posterior to the perichondral ossification center of the quadrate.

The dorsal limb of the hyoid arch — the hyo-symplectic — is broader dorsally than ventrally and remains joined to the neurocranium by some thin cartilage. A posterior cartilaginous opercular process is present at the broadest part of the hyo-symplectic cartilage and articulates with a small, thin opercle. A small foramen for the passage of the facial nerves pierces the center of the hyo-symplectic, in the region where the hyomandibula will later ossify. The antero-ventral part of the hyo-symplectic, the future symplectic, is narrow and far from the condyle of the pars quadrata.

In specimens of about 15 mm, the dermal ectopterygoid and entopterygoid appear. The thin, elongate ectopterygoid is lateral to the palatoquadrate, whereas the entopterygoid is medial to the palatoquadrate and located between the pars autopalatina and pars quadrata.

In 16.5—17 mm specimens, the autopalatine, metapterygoid, and quadrate (Fig. 4B) are partially ossified, however they are still joined by a large quantity of cartilage. The autopalatine has a large mass of cartilage anteriorly; some cartilage also separates the autopalatine from the entopterygoid. The metapterygoid is fan shaped, with a sharp cartilaginous processus basalis extending medially from the anterodorsal margin and perforated by a small foramen. The processus metapterygoideus lateralis is small and extends dorsally to lie lateral to the anteroventral membranous outgrowth of the hyomandibula. The quadrate is a small triangle bearing a long posteroventral process that lies almost horizontal to the body axis.

A small, elongate, thin ectopterygoid is posterior and ventral to the autopalatine and ventral to the palatoquadrate cartilage. The entopterygoid is elongate, broader anteriorly than postero-ventrally and has fine arachnoid projections that extend below the palatoquadrate cartilage.

The hyomandibula is almost totally ossified but remains joined by a large cartilage to the symplectic, and by a narrow cartilage to the interhyal. An elongate, ventrally directed, membranous process develops from the anterior margin of the hyomandibula.

In a 21 mm specimen, all bones of the suspensorium (Fig. 4C) are differentiated but still joined by large remnants of the palatoquadrate cartilage. In a 111 mm specimen, the degree of ossification is higher, but large areas of cartilage are still present between the autopalatine, metapterygoid, and quadrate.

In adults the autopalatine, metapterygoid, and quadrate (Fig. 4D) are thick bones with fine perichondral ossification surrounding large areas of chondroid bone.

The autopalatine is broadest anteriorly and has a slightly concave dorsal surface where the olfactory organ rests; the whole anterior margin of the autopalatine (Fig. 4D) is coated by an articular fibrocartilage with two articular facets, one for the lateral autopalatine-maxillary cartilage, and a medial articulation continuous with the eth-
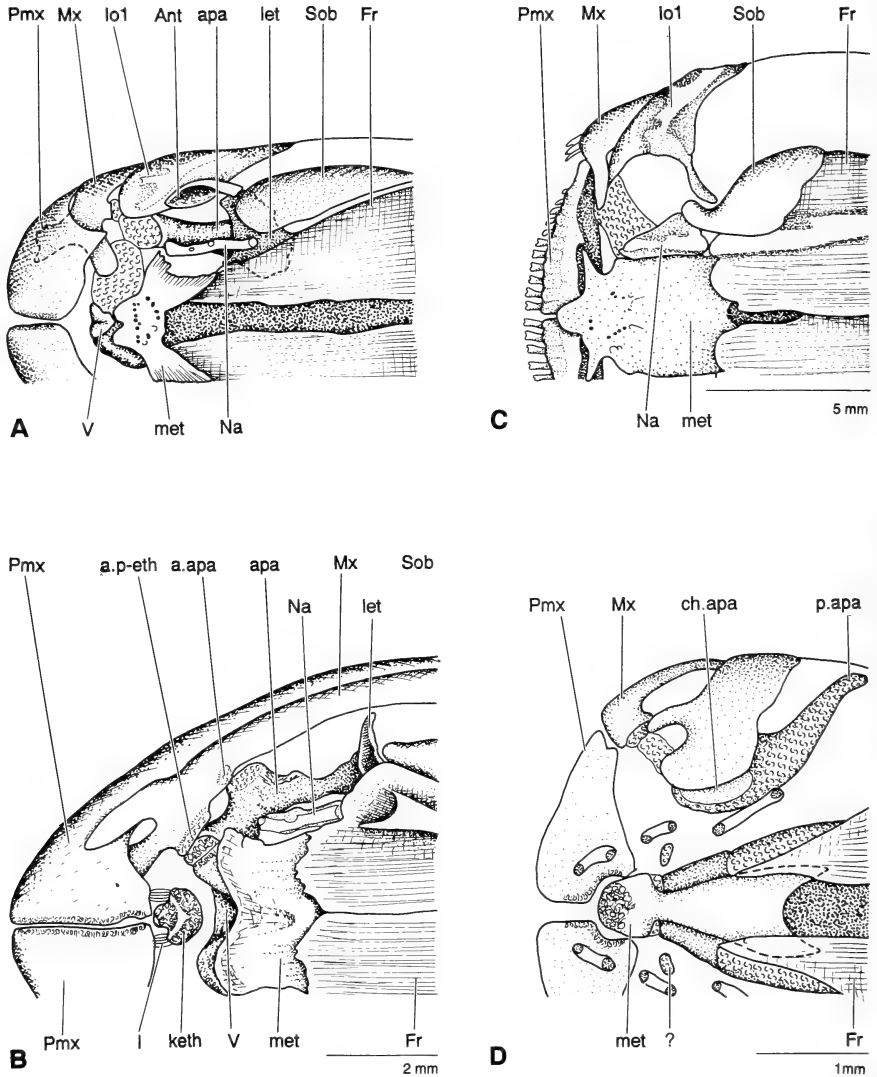
Fig.5: Relationships of the autopalatine of ostariophysans, dorsal view. — A: *Chanos chanos* (107.5 mm specimen; CAS-SU 38340); B: *Opsariichthys bidens* (74 mm standard length; PC 22); C: *Xenocharax spilurus* (94.9 mm standard length; CAS-SU 15639); D: *Hypopomus brevirostris* (133 mm total length; KU 13800). A-B, same scale.

a. apa: articular facet for autopalatine; Ant: antorbital; apa: autopalatine; a.p-eth: articular facet for preethmoidal cartilage; apa-mx: autopalatine-maxillary cartilage; ch. apa: chondroidal autopalatine; Fr: frontal; Io1: infraorbital 1; keth: kinethmoid; l: ligament; let: lateral ethmoid; met: mesethmoid; Mx: maxilla; Na: nasal; p.apa: pars autopalatina; Pmx: premaxilla; Sob: supraorbital; V: vomer; ?: unknown cartilage.

a.met-V

a.Mx

A

a.met-V-ch

a.let

B

a.met-V

a.let

a.Mx   a.V

C

a.let

D

a.Mx
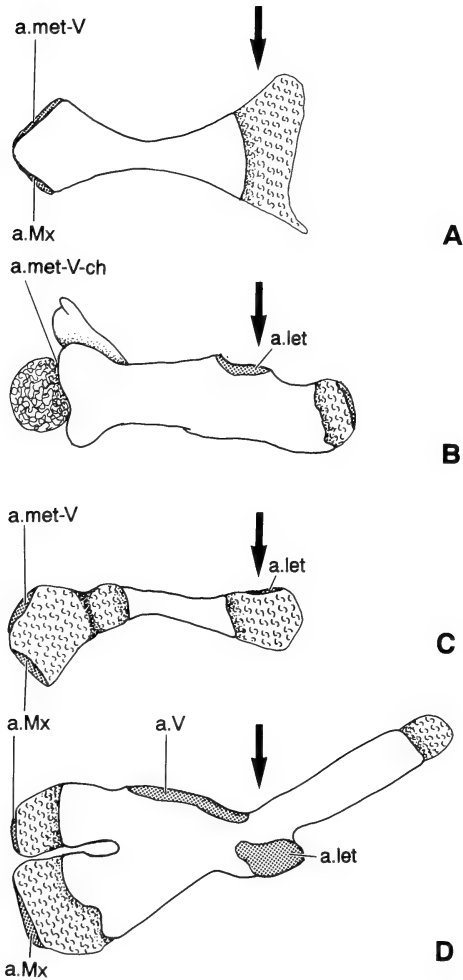
Fig.6: Articulatory surfaces of the autopalatine, left side, for cranial bones in ostariophysans. Arrows point to the position of the lateral ethmoid. — A: *Chanos chanos*; B: *Opsariichthys bidens*; C: *Xenocharax spilurus*; D: *Diplomystes camposensis*.
a.let: articular surface for lateral ethmoid; a.met-V: articular surface for mesethmoid and vomer; a.met-V-ch: articular surface for cartilaginous or chondroidal preethmoidal element connecting with mesethmoid and vomer; a.Mx: articular surface for maxilla; a.V: articular surface for vomer.

moidal cartilage. This ethmoidal chondroidal region is dorsal to the vomer and anteroventral to the mesethmoid. The autopalatine-maxillary cartilage is derived from the pars autopalatine, and is therefore not an ethmoidal element. (It was identified as an ethmopalatal cartilage by Fink & Fink 1981.) Both cartilages, the autopalatine-maxillary and the ethmoidal, become fibrocartilaginous during growth.

Anteriorly, the autopalatine (Figs. 5A, 6A) indirectly articulates with the lateral portion of the maxilla, and medially the autopalatine directly articulates with the neurocranium through the ethmoidal secondary cartilage or chondroidal region between the vomer
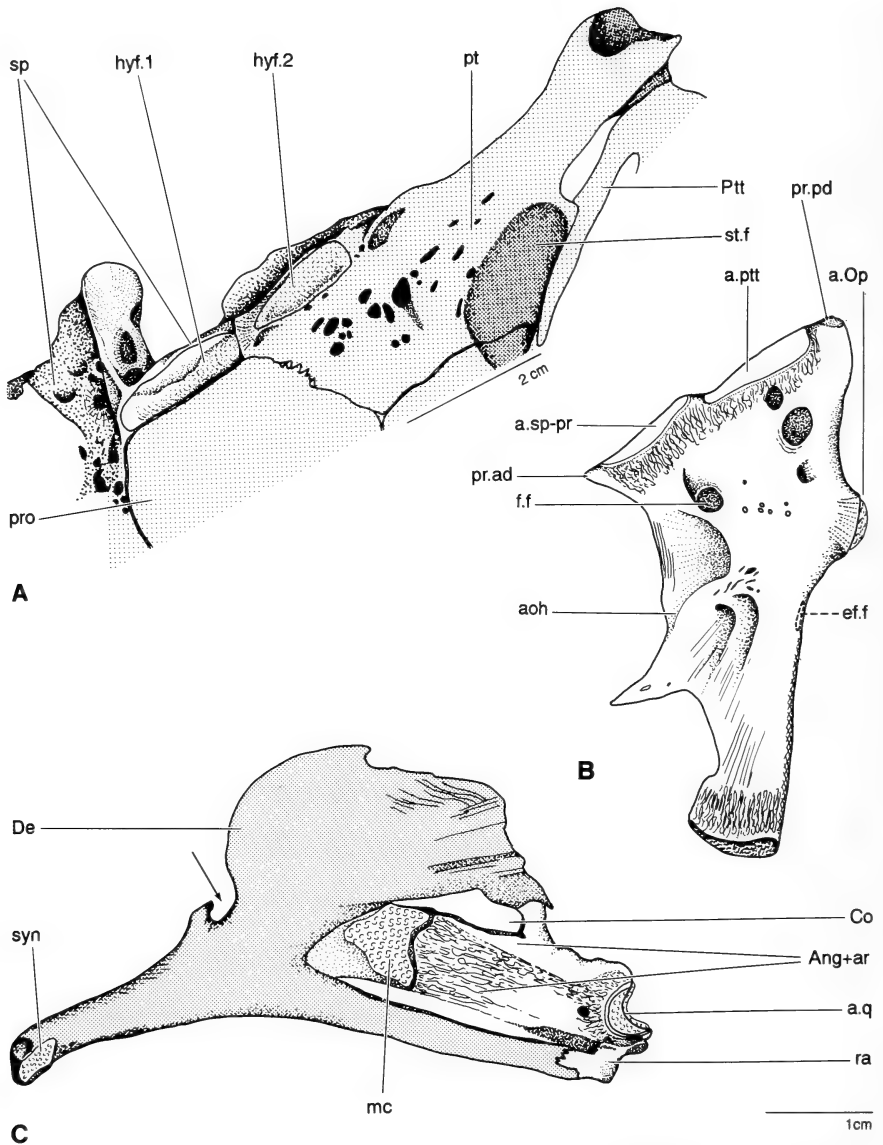
Fig.7: Part of the suspensorium and lower jaw of *Chanos chanos* (148 mm cranial length; CAS-SU 35075). —
A: Lateral region of the neurocranium, ventral view; B: Hyomandibula, medial view; C: Posterior part of the
lower jaw, lateral view. A, B, same scale. Arrow points to a notch.

Ang+ar: angulo-articular; aoh: anterior membranous outgrowth; a.Op: articular facet for opercle; a.pt: ar-
ticular facet for pterotic; a. sp-pr: articular facet for autosphenotic and prootic; a.q: articular facet for quadrate;
Co: coronomeckelian bone; De: dentary; hyf. 1-2: hyomandibular fossae 1-2; ef. f: foramen for exit of
hyoideomandibular nerve trunk; f.f: foramen for passage of hyoideomandibular nerve trunk; mc: Meckelian car-
tilage; Ptt: posttemporal; pr.ad: processus anterodorsalis; pr.pd: processus posterodorsalis; pro: prootic; pt:
pterotic; ra: retroarticular; sp: sphenotic; st.f: subtemporal fossa; syn: symphyseal surface.

and mesethmoid. The autopalatine does not articulate with the lateral ethmoid. The autopalatine-maxillary cartilage also laterally contacts infraorbital 1. The autopalatine sutures with the entopterygoid medially and ventrally, and with the ectopterygoid laterally and ventrally. The elongate, sharp, anterior portion of the ectopterygoid extends below the autopalatine.

The entopterygoid is slightly concave dorsally. It sutures with the autopalatine anteriorly, with the ectopterygoid and quadrate laterally, and with the metapterygoid posteriorly and medially. The suture between the entopterygoid and quadrate is relatively longer than in other teleosts, whose entopterygoids mainly suture with the ectopterygoids. In a lateral view of the suspensorium, the ectopterygoid is shaped like a boomerang; however, the whole bone is a complex shape, bearing a posterior projection medial to the quadrate and metapterygoid (Fig. 4D). Laterally, there is a schindylesis between the ectopterygoid and the anterior margin of the quadrate.

The metapterygoid is a small chondral bone without membranous outgrowths. It is joined by connective tissue to the anteroventral outgrowth and the anteroventral margin of the hyomandibula.

The quadrate has a fan-shaped body and a long posteroventral process. There is no medial groove for the symplectic, and the latter does not reach the body of the quadrate. The quadrate condyle articulates with the articular portion of a partially fused angular-articular-retroarticular (Fig. 7C). (This fusion was only observed in the largest specimen; only the angular and articular are fused in young specimens.) The quadrate condyle is expanded laterally and medially, with two slightly convex facets separated by a slight depression. The lateral facet is larger than the medial one. These articular facets fit in corresponding slightly concave facets of the articular; the angular and retroarticular portions of the jaw are excluded from the actual articulation. The posteroventral process of the quadrate is medial to the preopercle and sutured to it.

The hyomandibula (Figs. 4D, 7B) is the largest bone of the suspensorium. The main chondral portion is broader dorsally than ventrally. It bears two articular facets for the hyomandibular fossae of the neurocranium (Table 1). The larger anterior facet articulates with sphenotic (or autosphenotic) and prootic, and the posterior one with the pterotic (Fig. 7A). Both fossae are oval-shaped and separated by a notch. The anterior fossa is mainly formed by the autosphenotic; the prootic forms only the medial boundary, the pterotic forms the posterior border. The anterior facet is lower on the neurocranium than the posterior one, because the dorsal margin of the hyomandibula is obliquely ascending to the posterior.

The posterior margin of the hyomandibula bears a short opercular process for articulation with the opercle. Ventrally, the hyomandibula synchondrally articulates with the symplectic and interhyal. Posterolaterally the hyomandibula is overlapped by the anterior margin of the suprapreopercle and the preopercle.

The hyoideomandibular nerve trunk (Fig. 7B) penetrates the hyomandibula on the medial face, and then runs through the bone to exit the posterior margin, ventral to the opercular process. During ontogeny the foramen for the facial nerve which first opens laterally, becomes closed laterally (compare Figs. 4A—C, D).

Tab.1: Single or double articulation of the hyomandibula with cranial bones in some adult ostariophysans. Abbreviations for bones: phs: pterosphenoid; pro: prootic; pt: pterotic; sp: sphenotic. Bold types indicate fusion of bones.

	Single articulation				Double articulation					
					Anterior facet			posterior facet		
Chanos					-	sp	pro	-	-	pt
Carpiodes					phs	sp	pro	sp	pro	pt
Ctenopharyngodon					phs	sp	pro	sp	pro	pt
Cyprinus					phs	sp	pro	sp	pro	pt
Notropis					phs	sp	pro	sp	pro	pt
Ospariichthys					phs	sp	pro	sp	pro	pt
Ptychochceilus					phs	sp	pro	sp	pro	pt
Zacco					phs	sp	pro	sp	pro	pt
Cheirodon	-	sp	pro	pt						
Hoplias	-	sp	pro	pt						
Xenocharax	-	sp	pro	pt						
Bagre	-	sp	-	pt						
Callichthys	-	sp	-	pt						
Diplomystes	phs	sp	pro	pt						
Galeichthys	-	sp	-	pt						
Heptapterus	-	sp	-	pt						
Hypostomus	-	sp	-	pt						
Ictalurus	-	sp	-	pt						
Nematogenys	-	**sp**	**pro**	pt						
Noturus	-	sp	-	pt						
Ochmacanthus	-	sp	pro	pt						
Olivaichthys	phs	sp	pro	pt						
Parapimelodus	-	sp	-	pt						
Pylodictis	-	sp	-	pt						
Rhamdia	-	sp	-	pt						
Trichomycterus	-	**sp**	**pro**	pt						
Gymnotus	phs	sp	pro	pt						
Hypopomus	phs	sp	pro	pt						

The symplectic (Fig. 4D) is an elongate bone that in adults only articulates with the hyomandibula. The interhyal also articulates with the cartilage between the hyomandibula and symplectic.

The main ontogenetic changes in the suspensorium of *Chanos chanos* include: 1) the transformation of a semi-mobile joint between autopalatine and entopterygoid to a suture; 2) the development of a suture between the anterior part of the ectopterygoid and autopalatine; and 3) the posterior growth of the ectopterygoid medial to the metapterygoid.
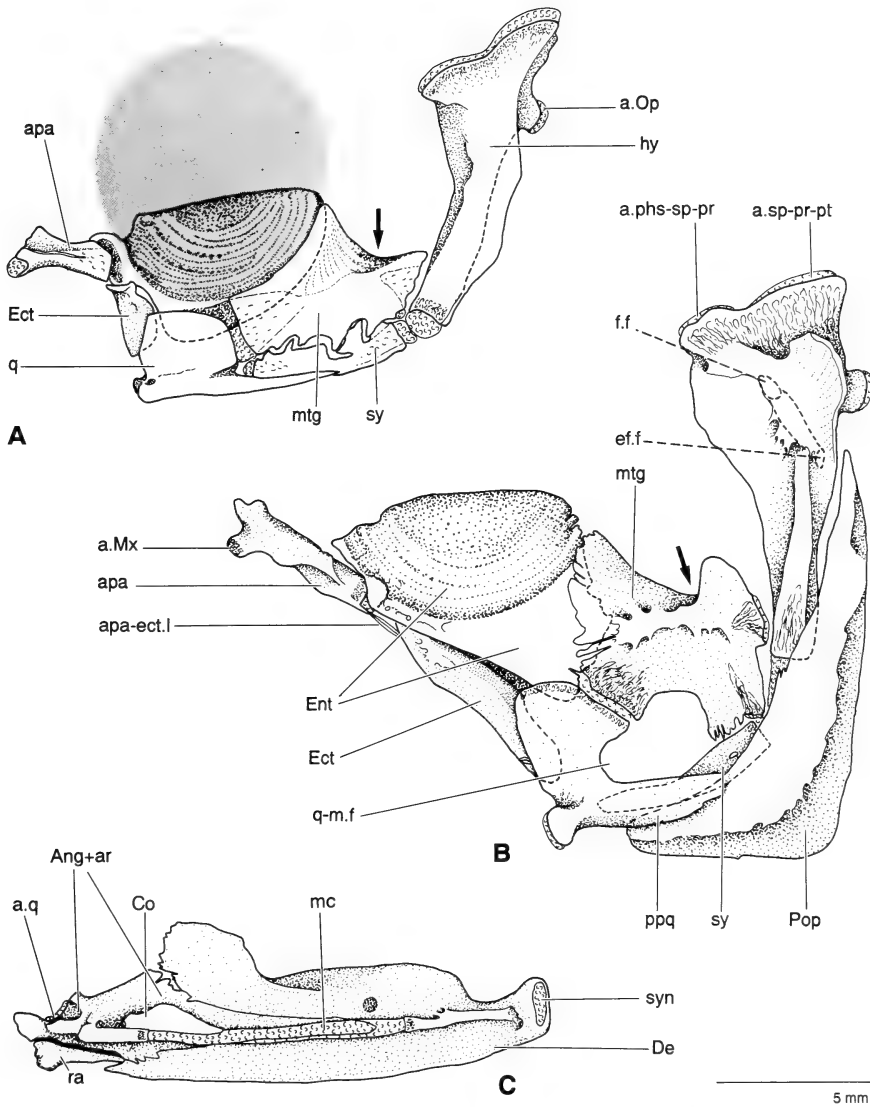
Fig.8: Suspensorium and lower jaw of *Opsariichthys bidens*; dotted area represents the position of the eye. —
A: Suspensorium, lateral view (26.5 mm standard length; PC 22); B: Suspensorium, lateral view (120 mm standard length; CAS-SU 32512); C: Lower jaw, medial view (120 mm standard length; PC 32512). Arrows point to a notch. Scale applies to the entire figure.
Ang+ar: angulo-articular; a.Mx; articular facet for maxilla; a.Op: articular facet for opercle; apa: autopalatine; apa-ect.l: autopalatine-ectopterygoid ligament; a.phs-sp-pr: articular facet for pterosphenoid, sphenotic, and prootic; a.sp-pr-pt: articular facet for autosphenotic, prootic, and pterotic; a.q: articular facet for quadrate; Co: coronomeckelian bone; De: dentary; Ect: ectopterygoid; Ent: entopterygoid; ef.f: exit of hyoideomandibular nerve trunk; f.f: foramen for passage of hyoideomandibular nerve trunk; hy: hyomandibula; mc: Meckelian cartilage; mtg: metapterygoid; Pop: preopercle; ppq: posteroventral process; q: quadrate; q-m.f: quadrate-metapterygoid fenestra; ra: retroarticular; sy: symplectic; syn: symphyseal surface.

Cypriniforms

The series of *Opsariichthys bidens* includes 10 specimens ranging from 26.5 mm to 118 mm standard length.

In a 26.5 mm specimen, all bones of the suspensorium (Fig. 8A) are perichondrally ossified; however, they retain a large quantity of cartilage inside the ossification. The autopalatine is small, with a tube-like body that broadens slightly posteriorly and anteriorly bears a concave articular facet for the maxilla. A thin, dorsal membranous outgrowth extends from the main body of the bone. The posterior cartilage of the autopalatine nests into a concave, broad articular facet of the entopterygoid. The entopterygoid forms the medial margin of the suspensorium and dorsomedially is largely concave; it also lies medial to the quadrate and metapterygoid.

The small, stout ectopterygoid anteriorly forms a thick margin that ventrally partially surrounds the articular facet of the entopterygoid. The posterior part of the ectopterygoid is less robust and medial to the quadrate.

The metapterygoid is the largest bone derived from the palatoquadrate cartilage. It bears a sharp, large processus basalis dorsally separated from the posterior margin of the bone by a notch. The posterior margin of the metapterygoid bears two short processes, each with an articular surface; the dorsal one abuts the anteroventral margin of the hyomandibula, the ventral one articulates with the cartilage between the hyomandibula and symplectic. The ventral margin of the metapterygoid is unusual in that it has a dentate suture with the symplectic (Fig. 9).

The quadrate has an almost fan-shaped body, with a moderately long posteroventral process. The symplectic does not reach the body of the quadrate. The condylar articulation for the lower jaw is anteriorly directed, in a plane almost horizontal to the neurocranium. This condyle articulates with the articular portion of the angulo-articular (Fig. 8A—C) of the lower jaw.

The hyomandibula (Fig. 8A) is vertically elongate; it has a lateral membranous outgrowth that extends along almost the entire length of the bone. There is a well-developed opercular process at the posterior margin, but any trace of an anterior process of the hyomandibula is lacking.

There are remarkable ontogenetic changes in the shape of some elements in the suspensorium and the lower jaw in *Opsariichthys*. The dentate suture between metapterygoid and symplectic begins to disappear in specimens of about 30 mm, and the form of the quadrate begins to change in specimens of about 30 mm.

In a 118 mm specimen, the autopalatine is well ossified; it anteriorly bears two articular surfaces (Figs. 5B, 6B, 8B); a lateral one for the maxilla and a medial one for the pre-ethmoidal cartilage. There is also a small dorsomedial articular surface for the lateral ethmoid, close to the posterior end of the autopalatine. Posterolaterally, the auto-palatine (Fig. 8B) has a small process where the short autopalatine-ectopterygoid ligament attaches. Posteriorly, the autopalatal fibrocartilage articulates with a medial concave facet on the entopterygoid.
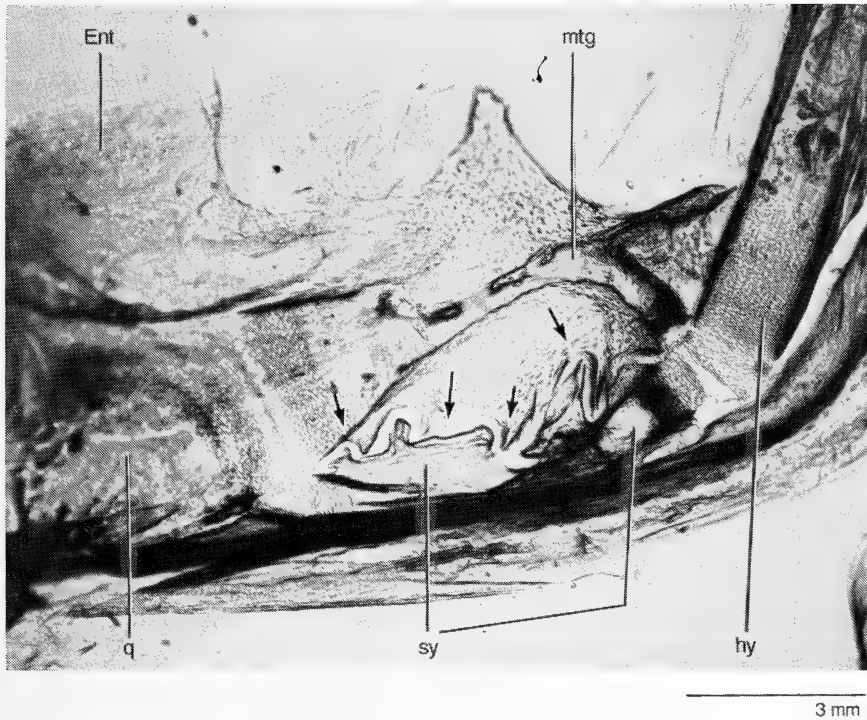
Fig.9: Lateral view of the suspensorium of *Opsariichthys bidens* illustrating the presence of a dentate suture between metapterygoid and symplectic that is indicated by arrows (26.5 mm standard length; PC 22).
Ent: entopterygoid; hy: hyomandibula; mtg: metapterygoid; sy: symplectic; q: quadrate.

The large entopterygoid slightly overlaps the posterior part of the autopalatine, which is unusual among teleosts. The posterior part of the entopterygoid is medial to the metapterygoid, and to a small area to the quadrate.

The elongate, blade-like ectopterygoid does not reach the autopalatine anteriorly, and it is medial to the quadrate posteriorly. A suture between the ectopterygoid and quadrate is missing, instead a short ligament connects them.

The metapterygoid is a large bone, with serrate or dentate anterior and posteroventral margins. It has a well developed processus basalis, separated by a notch from the posterior part of the bone. Anteroventrally, there is a synchondral joint between the metapterygoid and quadrate. A deep notch (part of the wall of the quadrate-metapterygoid fossa) separates the articular border with the quadrate from the serrated posteroventral margin. The posterior margin bears two articular surfaces; the dorsal one for the anteroventral part of the hyomandibula, the ventral one for the cartilage between the hyomandibula, symplectic, and interhyal.

The quadrate has a complex shape. The main body is separated by a deep notch from the posteroventral process; this process is broad and lateral to part of the anterior pro-

cess of the preopercle. The quadrate also forms part of the quadrate-metapterygoid fenestra.

The articular facet of the lower jaw (Fig. 8C) is composed of two well-developed convex surfaces separated by a notch; this condylar surface lies within the posteriorly directed, broad surface of the articular, that is almost smooth. The articular portion of the angulo-articular is small relative to the angular. The retroarticular is well-developed and doesn't reach the articular facet of the jaw.

The hyomandibula (Fig. 8B) of adults, retains the shape present in young individuals (Fig. 8A), but its dorsal margin is less inclined than in young individuals. There are two facets articulating with the neurocranium (Table 1). The anterior facet articulates with the pterosphenoid, sphenotic, and prootic; the posterior one with the autosphenotic, prootic, and pterotic. Anteriorly, the hyomandibula has a moderately large membranous outgrowth; posteriorly, there is a well-developed opercular process; laterally, there is a well-developed, but thin, membranous outgrowth.

The foramina for both the entrance and exit of the ramus hyoideomandibularis of the facial nerve (Fig. 8B) are medial. The nerve is enclosed in a short bony tube that opens to the posterior margin of the hyomandibula, ventral to the opercular process.

The suspensorium of *Opsariichthys* and *Zacco* are similar; however, the suture between the metapterygoid and symplectic observed in young specimens of *Opsariichthys* was not observed in young specimens of *Zacco*, and the quadrate-metapterygoid foramen is smaller in *Zacco* than *Opsariichthys*. The suspensorium of other cyprinids, as well as other cypriniforms, has the same general pattern described above for *Opsariichthys*. However, there is some variation in the shape and size of some bones and in the number of additional chondroids or bones between the autopalatine, the maxilla, and the ethmoidal region (e.g., Ramaswami 1955 a, b, 1957, Nelson 1969, Sawada 1982, Mayden 1989).

Characiforms

Two specimens of *Xenocharax* were studied. Their standard lengths are 75.9 and 94.9 mm. For more information and variation of the suspensorium among distichodontids see Daget (1961, 1967) and Vari (1979).

The autopalatine (Fig. 10A) is a small bone, rod-like, and slightly expanded posteriorly. It is mostly anterior to the lateral ethmoid. Anteriorly, the autopalatine bears a large, broadly-expanded cartilage (intermediating body that during ontogeny becomes the submaxillary cartilage of Bertmar 1959). In the 75.9 mm specimen, the cartilage is simple, whereas in the 94.9 mm specimen, the cartilage has differentiated into two distinct regions: an articular cartilage that nests into the anterior part of the autopalatine and an expanded part or the maxillary-autopalatine cartilage (Fig. 5C) that provides the contact between the suspensorium and the neurocranium and maxilla. Medially, the maxillary-autopalatine cartilage is tightly joined to the vomer and the cartilaginous area between the vomer and mesethmoid. Laterally, the maxillo-autopalatine cartilage articulates with the maxilla; anteriorly, the cartilage rests on the posterodorsal part of the premaxilla. Posteriorly, the autopalatine bears a large, oval-shaped cartilage that is
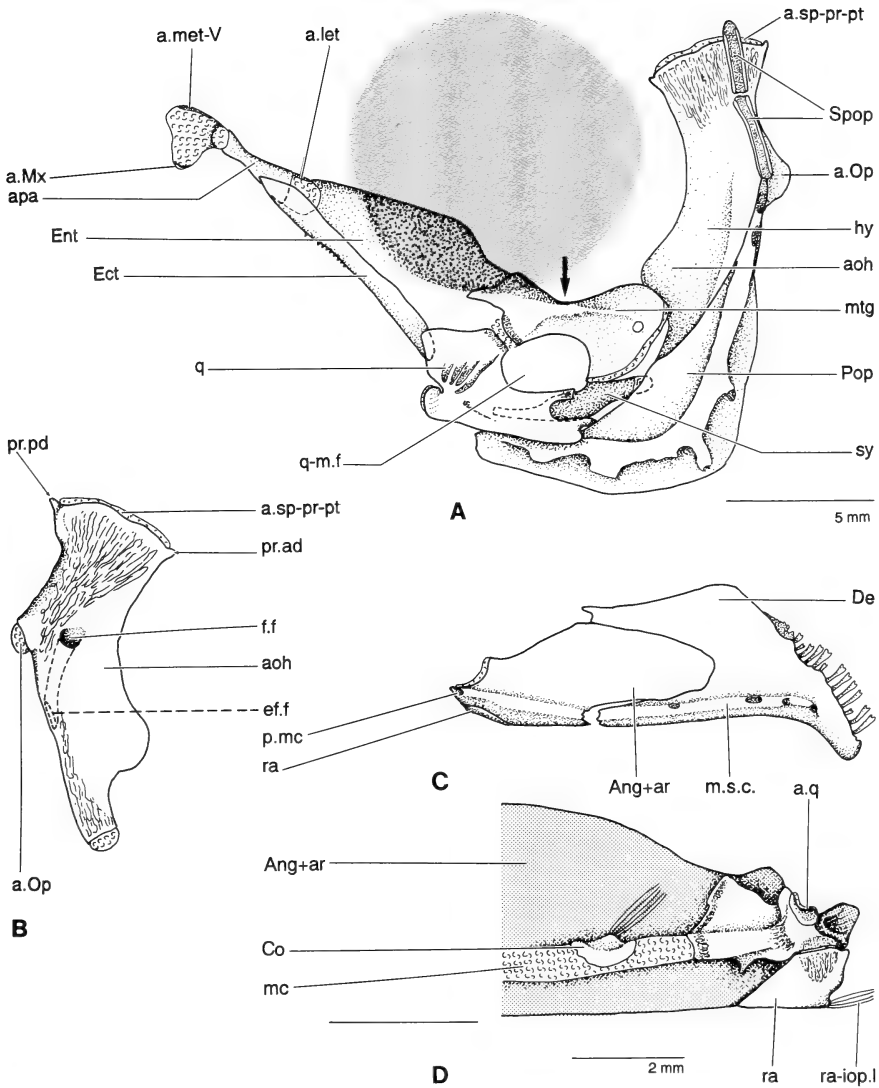
Fig.10: Suspensorium, preopercle, and lower jaw of *Xenocharax spilurus* (94.9 mm; CAS-SU 15639); dotted area represents the position of the eye. — A: Suspensorium, lateral view. Arrow points to a notch; B: Hyomandibula, medial view; C: Lower jaw, lateral view; D: Posterior part of lower jaw, medial view. A—C, same scale.

Ang + ar: angulo-articular; a.let: articular facet for lateral ethmoid; a. met-V: articular facet for cartilage joining mesethmoid and vomer; a.Mx: articular facet for maxilla; aoh: membranous outgrowth; a.Op: articular facet for opercle; apa: autopalatine; a.sp-pr-pt: articular facet for sphenotic, prootic, and pterotic; a.q: articular facet for quadrate; Co: coronomeckelian bone; De: dentary; Ect: ectopterygoid; ef.f: exit of hyoideomandibular nerve trunk; Ent: entopterygoid; f.f: foramen for passage of hyoideomandibular nerve trunk; hy: hyomandibula; mc: Meckelian cartilage; m.s.c.: mandibular canal; mtg: metapterygoid; p.mc: posterior opening of mandibular canal; Pop: preopercle; pr.ad: processus anterodorsalis; pr.pd: processus posterodorsalis; q: quadrate; q-m.f: quadrate-metapterygoid fenestra; ra: retroarticular; ra-iop.l: retroarticular-interopercular ligament; Spop: suprapreopercle; sy: symplectic.

dorsal to both the ectopterygoid and entopterygoid, and articulates with the lateral ethmoid. Posteriorly, the autopalatine is attached to the ectopterygoid. The autopalatine is not sutured to the entopterygoid.

The entopterygoid (Fig. 10A) is a large, thin bone, that is slightly concave dorsally. Laterally it is linked by connective tissue and a ligament to the ectopterygoid, and medially, there is a small suture with the quadrate and metapterygoid. The ectopterygoid extends from below the autopalatine to the quadrate; anteriorly it is a half-tube which encloses the posterior part of the autopalatine; posteriorly it is blade-like and medial to the quadrate. The ectopterygoid bears small teeth along half of its anterior margin.

The quadrate is similar in shape to that of large *Opsariichthys* (compare Figs. 8B, 10A), and the broad posteroventral process partially covers the lateral face of the anterior part of the preopercle. The quadrate-metapterygoid foramen is more or less oval-shaped, and of moderate size. The quadrate sutures anterodorsally and medially with the entopterygoid, and anteriorly with ectopterygoid. There is a synchondral joint between the posterodorsal corner of the main portion of the quadrate and the metapterygoid. There is a condylar joint between the angulo-articular (Fig. 10C—D) of the lower jaw and the quadrate.

The metapterygoid (Fig. 10A) also is similar to that of *Opsariichthys*, but the posterior processes are separated in *Opsariichthys*, but they are united to form a broad articular surface extending along the posterior margin of the metapterygoid in *Xenocharax*.

The hyomandibula (Fig. 10A, B) is a dorsoventrally long, narrow bone. It retains regions of chondroid bone and secondary cartilage close to the neurocranial articular surface, and along a narrow region close to the posterior margin. The slightly broad anterior region is membranous. Dorsally, there is only one narrow, long articular surface, almost horizontal to the neurocranium. Anteriorly it articulates with the sphenotic and prootic, and posteriorly with the pterotic. About half way up the posterior margin of the hyomandibula is a rudimentary opercular process bearing a small, round articular surface. Ventrally, the hyomandibula articulates with the symplectic and interhyal.

The medial foramen for the hyoideomandibular nerve trunk (Fig. 10B) is almost in the middle of the bone. The nerve runs through a short tube in the hyomandibula exiting to the posterior margin, ventral to the opercular process.

The symplectic (Fig. 10A) is elongate, almost reaching the condylar region of the quadrate.

The suspensorium of *Hoplias* shows the general pattern of the suspensorium as in *Xenocharax*; however, *Hoplias* differs from *Xenocharax* and other characiforms in the presence of an almost triangular autopalatine (Fig. 11) that ventrally bears a small toothplate (see below). The autopalatine is a small bone that anteromedially has a short articular surface for the vomer, and a long facet for the lateral ethmoid posterodorsally. Posterolaterally, the autopalatine is sutured to the ectopterygoid. Laterally, the autopalatine articulates with the maxilla; and in addition, a short ligament keeps both bones
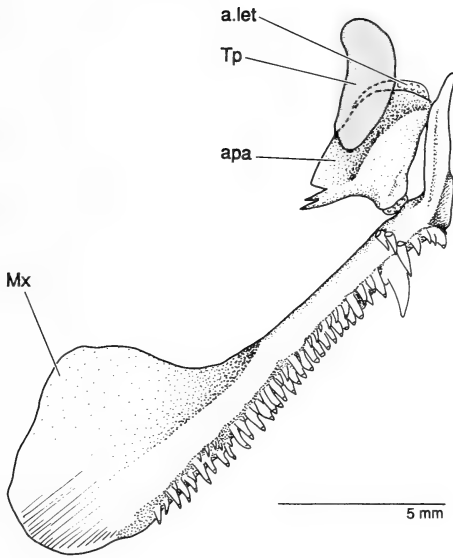
Fig.11: Anterior part of the suspensorium and maxilla of *Hoplias malabaricus*, ventral view (100 mm standard length; KU 13636).
a.let: articular facet for lateral ethmoid; apa: autopalatine; Mx: maxilla; Tp: toothplate (dotted).

in position. The autopalatine is dorsal to the entopterygoid; these bones do not articulate and are not linked by a ligament.

In *Hoplias*, the toothplate is attached by a ligament to the ventral part of the vomer and dorsal part of the autopalatine. This plate was called accessory ectopterygoid tooth plate by Weitzman (1964). It is anterior to but not associated with the ectopterygoid; the numerous, conical teeth face their antimeres medially; however, the toothplates are not sutured to each other. This small dentate bone is not a dermopalatine because this element is missing in primitive ostariophysans; therefore, this element is considered here to be a new formation. The name toothplate is used to avoid confusion with either the dermopalatine, or the subautopalatine toothplate of catfishes.

Gymnotoids

The suspensorium of gymnotoids has been extensively illustrated by Chardon & de la Hoz (1974), who proposed a classification of the group based on the suspensorium. Here I will only address a few points.

The anterior part of the palatoquadrate — the pars autopalatina — does not differentiate into an autopalatine in most gymnoids (Fig. 12A); however, it does in *Hypopomus* (Fig. 12B, D). In *Hypopomus*, anteriorly the suspensorium is connected to the premaxilla by a ligament; laterally, the pars autopalatine articulates with the maxilla. A small, round cartilage between the autopalatine and lateral ethmoid is present in *Hypopomus*. This cartilage is free. The ectopterygoid is absent. The large entopterygoid occupies the position of the ectopterygoid of other teleosts. Among gymnotoids, the dorsal projection of the entopterygoid (Fig. 12A, B) exhibits different degrees of development. This dorsal projection articulates with the lateral ethmoid, the cartilage between the lateral
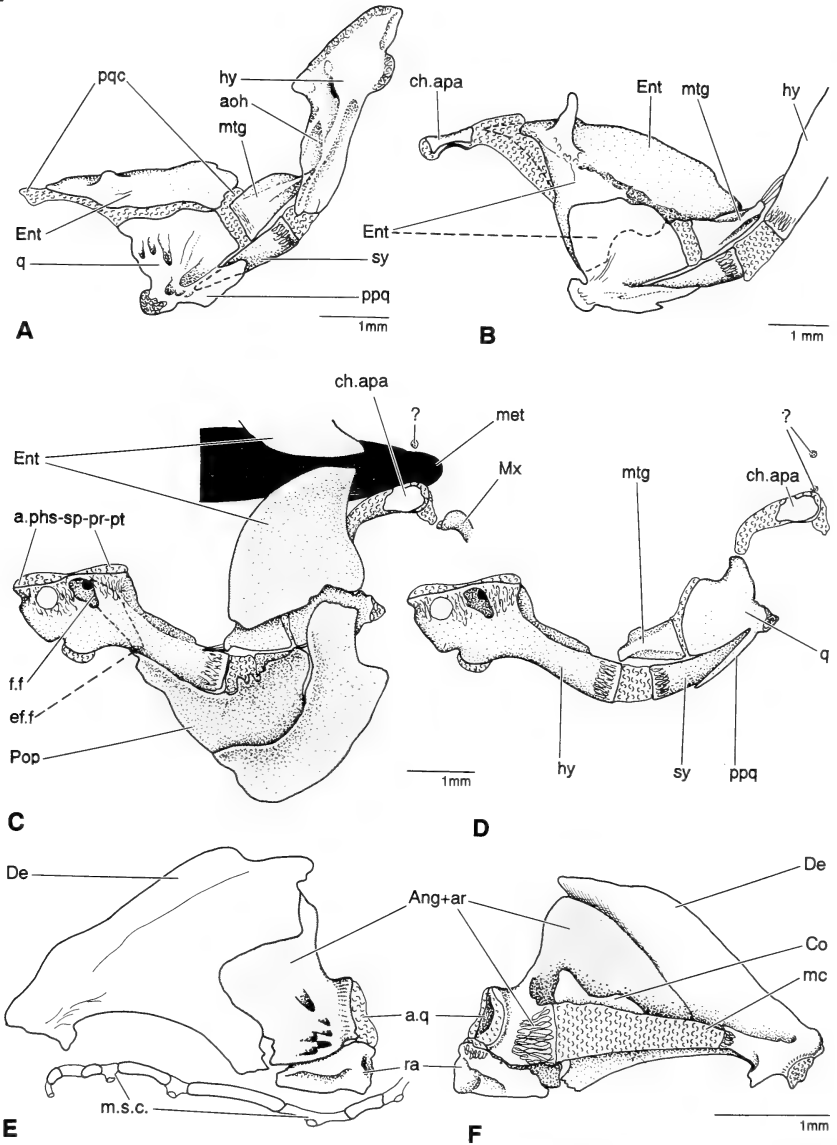
Fig.12: Suspensorium and lower jaw of gymnotoids. — A: *Gymnotus carapo*, lateral view (80 mm specimen; KU 13793); B—F: *Hypopomus brevirostris* (72 mm specimen; KU 13800); B: Suspensorium, lateral view; C: Suspensorium and related bones, medial view; D: Chondral elements of the suspensorium, medial view; E: Lower jaw, lateral view; F: Lower jaw, medial view. C—F same scales.

Ang+ar: angulo-articular; aoh: membranous outgrowth; apa: chondral autopalatine; a. phs-sp-pr-pt: articular facet for pterosphenoid, sphenotic, prootic, and pterotic; a.q: articular facet for quadrate; ch. apa: chondroidal autopalatine; Co: coronomeckelian bone; De: dentary; Ect: ectopterygoid; ef.f: exit of hyoideomandibular nerve trunk; Ent: entopterygoid; f.f: foramen for passage of hyoideomandibular nerve trunk; hy: hyomandibula; Iop: interopercle; mc: Meckelian cartilage; m.s.c.: mandibular canal; met: mesethmoid; mtg: metapterygoid; Mx: maxilla; Pop: preopercle; ppq: posteroventral process; pqc: palatoquadrate; q: quadrate; ra: retroarticular; sy: symplectic; ?: unknown cartilage.

ethmoid and orbitosphenoid, and/or the orbitosphenoid alone. Both right and left entopterygoids project medially and almost contact each other, ventral to the parasphenoid, in *Hypopomus*. The entopterygoids, however, do not project below the parasphenoid so extensively in *Gymnotus*. The metapterygoid in *Hypopomus* is small and slightly triangular. The posterodorsal part of the metapterygoid is medial to the hyomandibula and has a ligamentous connection between the metapterygoid and the posterior ceratohyal.

The quadrate (Fig. 12A—F) of gymnotoids articulates with the articular part of the angulo-articular and with the large retroarticular. Part of the quadrate condyle rests on the retroarticular when the fish closes its mouth.

The hyomandibula (Fig. 12A, B; Table 1) of gymnotoids has only one articular surface for the neurocranium; it articulates anteriorly with the pterosphenoid, sphenotic, and prootic, and posteriorly with the pterotic. Only a single hyomandibular facet is observed in the cranium, and the facet narrows posteriorly between the sphenotic-prootic region and the pterotic. I have not had the opportunity to examine specimens larger than 220 mm. Examination of larger specimens will be necessary to verify whether there is a change from a single articular facet to two articular facets during growth.

The hyoideomandibular nerve trunk (Fig. 12C, D) medially enters the hyomandibula and exits at the posterior margin of the bone, ventral to the opercular process.

Let us now examine the situation in catfishes.

SUSPENSORIUM OF CATFISHES

Regan (1911) used the presence or absence of certain pterygoid bones as distinguishing features of particular catfish families. Furthermore, he also used the type of pterygoid (the 'ectopterygoid') and entopterygoid (the 'entopterygoid') articulation to separate subfamilies within the Bagridae; and the presence or absence of the 'ectopterygoid' to separate genera within the Pimelodidae. He also mentioned the ligamentous connections of some pterygoid bones to the autopalatine, vomer, lateral ethmoid, and orbitosphenoid for some families. The connections he mentioned differ between groups; for example, ligaments join the 'entopterygoid' to the metapterygoid and vomer in *Diplomystes* (considered an unique feature by Alexander 1965; I will present contrary evidence here), whereas ligaments join the 'entopterygoid' to the metapterygoid and lateral ethmoid in the Doradidae.

From Regan (1911) to Fink & Fink (1981), the literature shows a variety of shapes and positions for bones that have been variously called the pterygoid or ectopterygoid, and others that have been called the entopterygoid, endopterygoid or mesopterygoid; all of which makes it difficult to precisely identify the elements. The question arises as to which of these bones are homologous within catfishes, and homologous with other
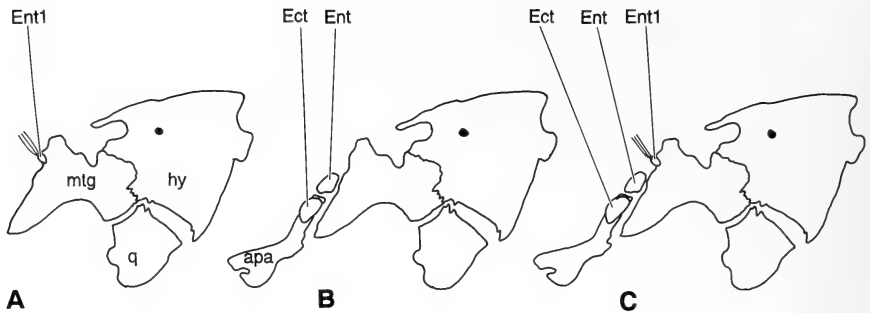
Fig.13: Identification of the dermal pterygoid bones in a diagrammatic medial view of the suspensorium of diplomystids according to various authors. — A: Regan (1911); B: Fink & Fink (1981); C: present paper. apa: autopalatine; Ect: ectopterygoid; Ent: entopterygoid; Ent1: 'entopterygoid' type 1; hy: hyomandibula; mtg: metapterygoid; q: quadrate.

teleosts. Gosline (1975: 3) distinguished two problems concerning the names applied to the bones of catfishes (1) nomenclatural and (2) zoological (the difficulty in identification of elements between divergent taxa). Figure 13A—C, based on diplomystids, illustrates both problems. Regan (1911) and Fink & Fink (1981), agreed only in the identification of the metapterygoid. In addition, the ligamentous connections of the metapterygoid are somewhat different from that stated by Regan (see Arratia 1987a, and below for diplomystids).

According to Regan (1911: 7) the ectopterygoid is absent in *Diplomystes*, a small entopterygoid is present (Fig. 13A) that connects the metapterygoid to the vomer, and furthermore the metapterygoid is anteriorly attached to the autopalatine and medially to the orbitosphenoid. Alexander (1965) and Fink & Fink (1981) agreed that the ectopterygoid and entopterygoid are both present in *Diplomystes*, but the element which Fink & Fink (1981: Fig. 32B) identified as the entopterygoid is not homologous with the entopterygoid of Regan (1911) and Alexander (1965). This is because the entopterygoid of Fink & Fink lacks the ligamentous connection to the cranium and has a unique position in relation to the autopalatine. I have only seen a few specimens that have had the entopterygoid like that described by Regan (Fig. 13A, C).

When this type of 'entopterygoid' is present, it is in addition to two other bones that correspond to the ectopterygoid and entopterygoid of Lundberg (as cited in Gosline 1975) and Fink & Fink (1981). The entopterygoid described by Regan and Alexander is commonly absent; and when it is present, is very small. The bone forming a cup-like ossification around the distal cartilage of the autopalatine has been labelled as the mesopterygoid or endopterygoid (Regan 1911, Lundberg cited in Gosline 1975, Fink & Fink 1981); whereas Alexander (1965: Fig. 4, top) labelled it as the ectopterygoid. I have named this bone as bone 4 (Arratia 1987a), following McMurrich (1884a). The 'entopterygoid' is often absent from one or both sides of the body and so is the ectopterygoid of Fink & Fink (1981). I considered this element not to be homologous with the entopterygoid, because its position and relationships differ from those of other teleosts (Arratia 1987a).

In my opinion, the identification of the pterygoid bones in catfishes is difficult for a variety of reasons: some elements are not consistently present, some are so enlarged that they occupy what would otherwise be the position of two or three pterygoid bones in other teleosts (see below), some have ligamentous connections that vary between groups, and some elements are new formations such as the rudimentary dermal pterygoids.

In addition, siluroids may have between three (e.g., diplomystids, parapimelodids) and zero (e.g., trichomycterids, callichthyids some ictalurids, synodontids) pterygoid elements. These elements include sesamoid 'entopterygoid' types 1—7 and additional pterygoid type 1. The fact that some siluroids have more than two dermal and/or tendon bones and sesamoid pterygoids shows that the palatal region of those siluroids differs from other ostariophysans. It is extremely difficult to determine which pterygoids are homologous with the traditionally recognized dermal ectopterygoid or dermal entopterygoid of other ostariophysans without developmental studies. My attempt to establish homology for the additional dermal and/or sesamoid pterygoids of siluroids with the ectopterygoid of other ostariophysans failed when considering only the macromorphology of the suspensorium. However, to surrender and consider the sesamoid 'entopterygoid' types 1—7 as just the entopterygoid, is too simplistic an ap-
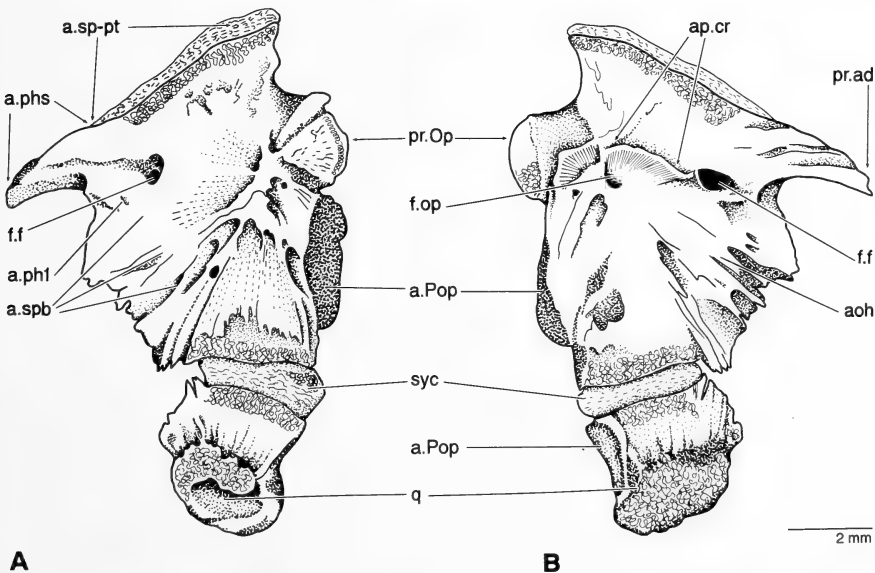
Fig.14: Posterior part of the suspensorium of *Diplomystes camposensis*. (Disarticulated specimen; PC 110276). — A: medial view; B: external view.

a.lj: articular facet for lower jaw; aoh: anterior membranous outgrowth; a.Op: articular facet for opercle; ap. cr: levator autopalatini crest; a. ph1: attachment area of pharyngobranchial 1; a.phs: articular facet for pterosphenoid; a.Pop: articular facet for preopercle; a. spb: attachment area for pseudobranch; a.sp-pt: articular facet for sphenotic and pterotic; f.f: foramen for passage of hyoideomandibular nerve trunk; f.op: foramen for passage of ramus opercularis; hy: hyomandibula; pr. ad: processus anterodorsalis; pr. Op: processus opercularis; q: simple quadrate; syc: symplectic cartilage.

proach. The sesamoid 'entopterygoid' types 1—7 are not strictly identical with the entopterygoid of other ostariophysans, and the relationships of the 'entopterygoid' with the surrounding elements differs between the catfish groups. It is therefore important to define the 'entopterygoid' type according to its ligamentous connections, because these connections differ in the palatal region of catfishes. Examples of the variation in the 'entopterygoid' include the following: a large bone contacting the hyomandibula posteriorly, the lateral ethmoid anteriorly and projecting lateral to autopalatine (e.g., *Amplyceps mangois*; Tilak 1967); a small crescentic bone (e.g., in 'pimelodids'); the 'entopterygoid' is absent (e.g., in trichomycterids; Arratia 1990a).

The absence of the symplectic bone has been traditionally accepted for catfishes; nevertheless, Howes (1983a: Fig. 23) illustrated the presence of a small cartilaginous symplectic between the hyomandibula and quadrate in *Hypophthalmus*. In a few large specimens of *Diplomystes camposensis* (Fig. 14A, B; see below), I have found a large dense cartilage exhibiting some ossification. This cartilage is between the hyomandibula and quadrate. I therefore consider it to be the remnant of the symplectic cartilage. In all siluroids there is a large cartilage between the hyomandibula and quadrate.

A small, triangular quadrate lacking an ossified anterior pterygoid process (identified herein as simple quadrate; Figs. 14A, B, 15A) is present in some siluroids such as diplomystids, ictalurids, and nematogenyids (Arratia 1990a: Fig. 12A, B), and modified slightly (to become longer) in loricariids and callichthyids (Arratia 1990a: Figs. 13A, B). In other catfishes, there is a complex-shaped element (Fig. 15B) with two well ossified chondral regions similar to those of both the quadrate and an ossified anterior pterygoid process; a membranous outgrowth may develop between both regions during
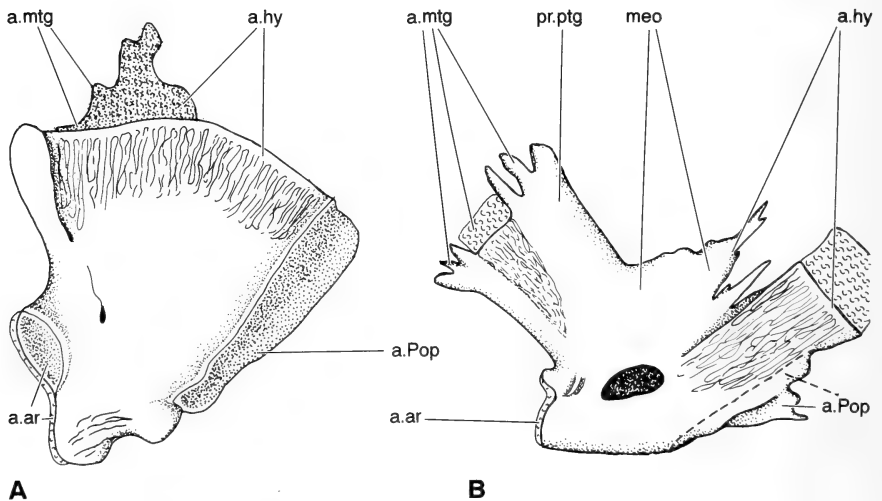
Fig.15: Quadrate of catfishes. — A: Simple quadrate; B: Complex quadrate.
a.ar: articular facet for articular; a.hy: articular facet for hyomandibula; a.mtg: articular facet for metapterygoid; a. Pop: articular facet for preopercle; pr. ptg: processus pterygoideus; meo: membranous outgrowth.

ontogeny. I have named this element the complex quadrate (Arratia 1990a); it has been named as bifid quadrate by Ferraris (1988) and Lundberg et al. (1991). The presence of a simple quadrate or a complex quadrate results in an important difference in the place-ment of the metapterygoid (Arratia 1990a; see below).

I cannot describe the morphology of the suspensorium for all catfishes. I therefore in-tend to present what I have learned studying growth series of many individuals of a few species of catfishes. It may be instructive to remember that the confusion of Gosline (1975) in trying to understand the suspensorium of catfishes, is a reality for everyone who compares several catfish groups.

In the next section I will first describe the suspensorium of some siluroids with a simple quadrate: the diplomystids *Diplomystes* and *Olivaichthys*, the fossil hypsidorid *Hyp-sidoris*, the ictalurid *Ictalurus*, and the nematogenyid *Nematogenys*. This section is then followed by the description of fishes with a complex quadrate: the ictalurid *Noturus*, the 'pimelodids' *Heptapterus, Rhamdia*, and *Parapimelodus*, and the schilbeid *Eutro-piichthys*.

Siluroids with a simple quadrate

Diplomystids

As already established by Arratia (1987a: 25, 54, 97—99), the pterygoid series in diplomystids is variable in number and often varies between the left and right sides. Therefore, for the purposes of this paper, I have chosen *Diplomystes* specimens with a 'complete' suspensorium and compare them with that of the Argentinean diplomystid *Olivaichthys viedmensis*.

The series of *Diplomystes* includes four specimens of *D. chilensis*, 12 cleared and stain-ed specimens of *D. camposensis*, and six specimens of *D. nahuelbutaensis*. The speci-mens range from 23 mm to 210 mm standard length. The series of *Olivaichthys* examin-ed includes five cleared and stained specimens, ranging from 28 to 206 mm.

In a 23 mm specimen of *Diplomystes*, the suspensorium is partially ossified. The autopalatine (Fig. 16A) is separate from the hyo-symplectic-pterygoquadrate plate; the partially ossified elements are still joined by large areas of cartilage. The anterior car-tilage of the autopalatine is bifid anteriorly and the elongate medial projection overlaps the maxilla. A small, semi-cylindrical ectopterygoid is attached to the posteroventral part of the autopalatine. This small bone (which may or may not be present) does not have the position or relationship of the ectopterygoid of most other teleosts, and I therefore described it as an additional pterygoid (Arratia 1987a). However, upon study-ing more material (particularly of *Chanos* and *Xenocharax*) I must accept that this ele-ment is a reduced ectopterygoid. This is because the ectopterygoid in primitive ostariophysans and diplomystids is partially or mostly ventral to the autopalatine (see Figs. 4D, 10A). Another small, rudimentary pterygoid (which may or may not be pre-sent) arises as a cup-like dermal ossification around the distal part of the cartilaginous, rod-like autopalatine. This ossification is interpreted here as the entopterygoid through comparison with the entopterygoid in gonorynchiforms, cypriniforms, and characi-forms.
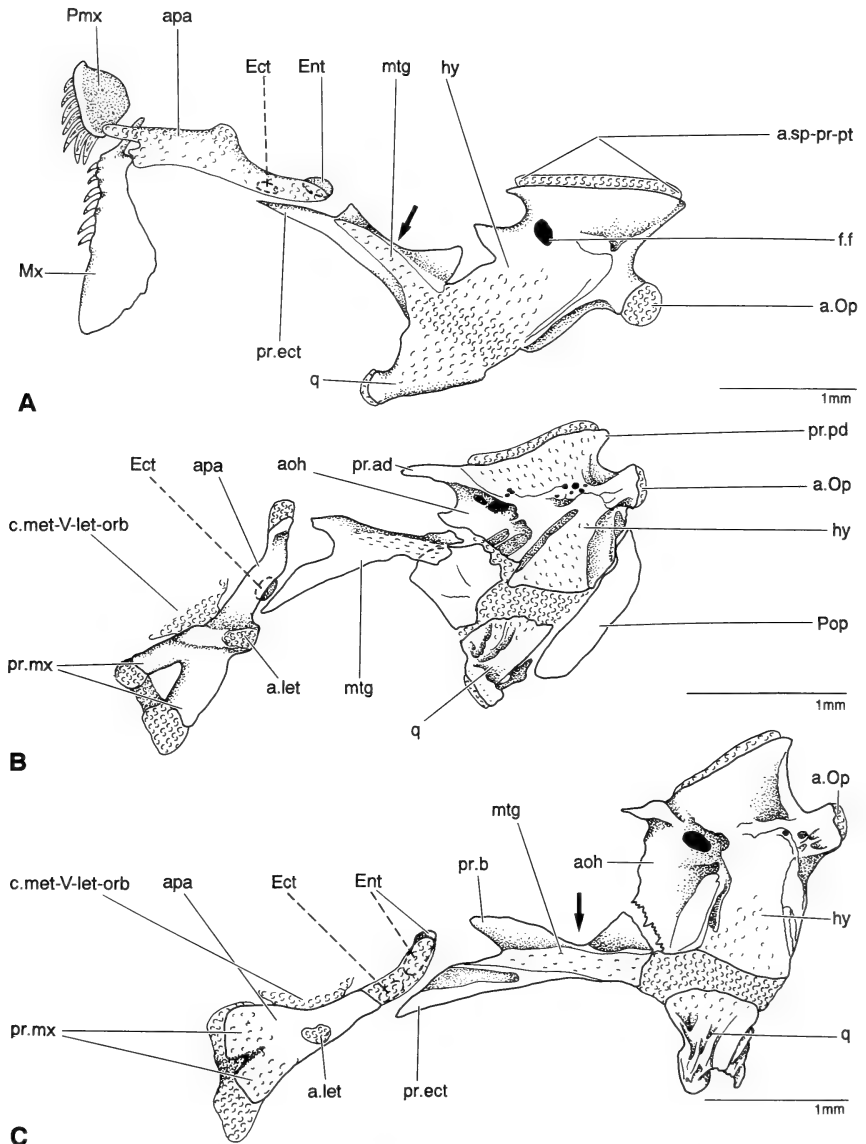
Fig.16: Suspensoria of diplomystids, lateral view. — A: *Diplomystes nahuelbutaensis* (23 mm standard length; PC 230186); B: *Diplomystes camposensis* (28 mm standard length; after Arratia 1987); C: *D. camposensis* (about 29 mm standard length; after Arratia 1987). Arrows point to a notch.

apa: autopalatine; a.let: articular facet for lateral ethmoid; aoh: anterior membranous outgrowth; a.Op: articular facet for opercle; a.sp-pr-pt: articular facet for sphenotic, prootic, and pterotic; apa: autopalatine; c. met-V-let-orb: cartilage joining mesethmoid, vomer, lateral ethmoid, and orbitosphenoid; Ect: ectopterygoid; Ent: entopterygoid; f.f: foramen for passage of hyoideomandibular nerve trunk; hy: hyomandibula; mtg: metapterygoid; Mx: maxilla; Pop: preopercle; pr.ad: processus anterodorsalis; pr.b: processus basalis; pr. ect: processus ectopterygoideus; Pmx: premaxilla; pr.mx: processus maxillaris; pr.pd: processus posterodorsalis; q: quadrate.

The metapterygoid is elongate, with a central rod of ossifying cartilage, and with a well ossified, elongate processus ectopterygoideus. Medially, the bone is thinly ossified. There is a slight notch separating the sharp, short processus basalis from the postero-dorsal flange of the bone. Metapterygoid, quadrate, and hyomandibula are broadly joined by cartilage of the hyo-symplectic-pterygoquadrate plate.

The simple, triangular quadrate is mainly ossified at its condylar articular facet with the lower jaw, and posteroventrally, at the articular facet with preopercle.
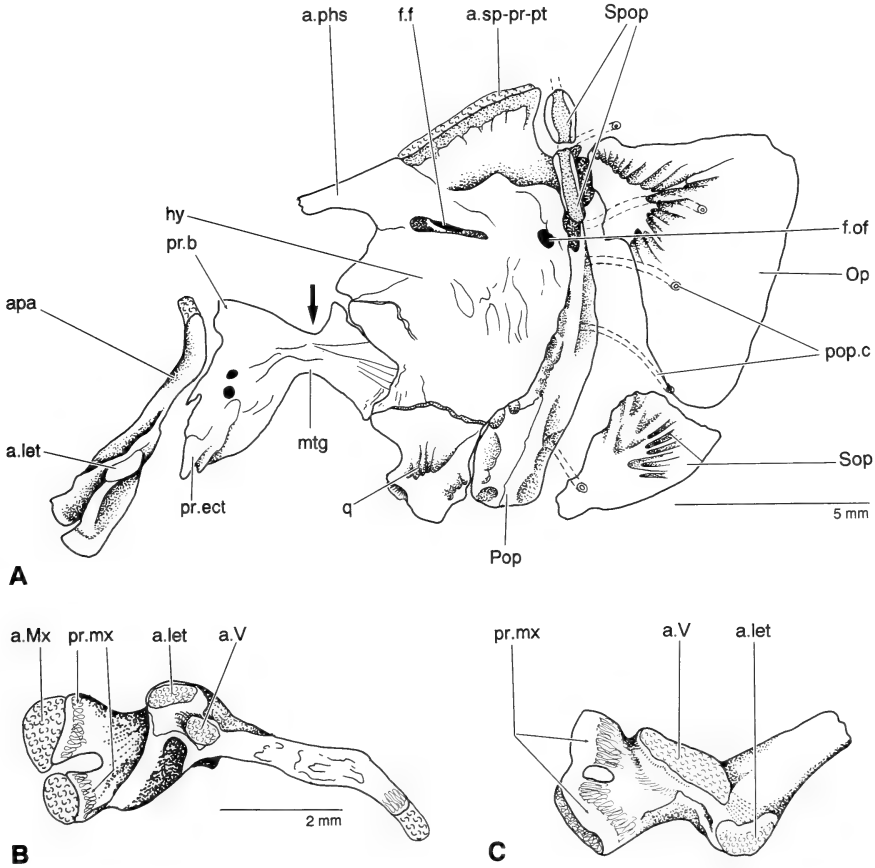
Fig.17: Suspensorium in diplomystids (after Arratia 1987a). — A: Suspensorium of *Diplomystes camposensis*, lateral view; note the absence of entopterygoid and ectopterygoid; B: Autopalatine of *D. camposensis*, right side, dorsal view; C: Autopalatine of *D. chilensis*, left side, dorsal view. Arrow points to a notch.

a.let: articular facet for lateral ethmoid; a.Mx: articular facet for maxilla; apa: autopalatine; a.phs: articular facet for pterosphenoid; a.V: articular facet for vomer; a.sp-pr-pt: articular facet for sphenotic, prootic, and pterotic; f.f: foramen for passage of hyoideomandibular nerve trunk; f.rop: foramen for ramus opercularis; hy: hyomandibula; mtg: metapterygoid; Op: opercle; Pop: preopercle; pop. c: preopercular canal; pr.b: processus basalis; pr.ect: processus ectopterygoideus; pr.mx; processus maxillaris; q: quadrate; Sop: subopercle; Spop: suprapreopercle.

The hyomandibula is a broad bone, with a long articular facet covered with cartilage and articulating with the sphenotic and pterotic. A small, short, sharp, membranous outgrowth extends anteriorly. Posteriorly, there is an elongate, massive opercular process and an elongate sutural surface at the posterolateral margin of the hyomandibula, below the opercular process. A small levator arcus palatini crest is present close to the posterior margin of the bone. A single foramen for both the entrance and exit of the facial nerve pierces the bone, close to the anterodorsal corner of the hyomandibula.

In a 28 mm specimen of *D. camposensis*, there is a large bone (Fig. 16B) on both sides of the body between the hyomandibula, quadrate, and metapterygoid and it was identified as ?metapterygoid by Arratia (1987a: 54, Fig. 25A). Based on my more recent
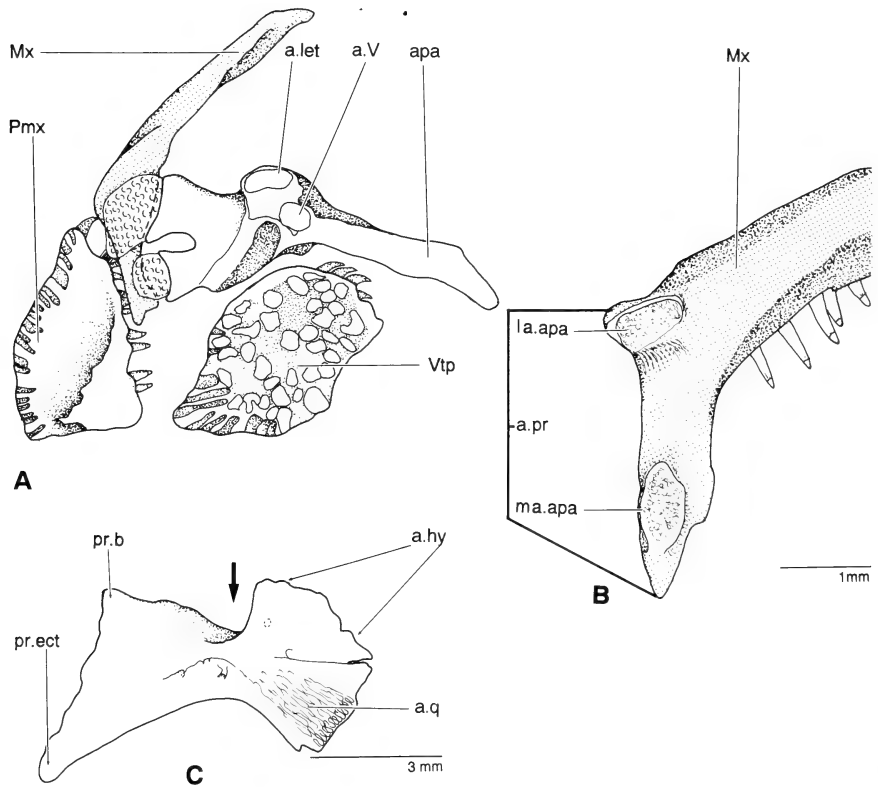
Fig.18: Elements of the suspensorium and maxilla in diplomystids. — A: Autopalatine and surrounding bones in *Diplomystes camposensis*, dorsal view (after Arratia 1987a); B: Anterior part of maxilla in *D. nahuelbutaensis* (CAS-SU 55425); C: Metapterygoid in *D. nahuelbutaensis*, lateral view (CAS-SU 55425). Arrow points to a notch.
a.let: articular facet for lateral ethmoid; a.hy: articular surface for hyomandibula; apa: autopalatine; a.pr: articular process of maxilla; a.q: articular surface for quadrate; a.V: articular facet for vomer; la.apa: lateral articular facet for autopalatine; ma.apa: medial articular facet for autopalatine; Mx: maxilla; Pmx: premaxilla; pr. b: processus basalis; pr.ect; processus ectopterygoideus; Vtp: vomerine toothplate.

comparative studies, I now consider this element as a result of a fracture of the hyo-symplectic-pterygoquadrate plate, which has grown as a separate element. This frac-tured piece may be part of the metapterygoid by origin or part of the anterior mem-branous outgrowth of the hyomandibula. In a 29 mm specimen of *D. camposensis*, all of the bones of the suspensorium are well ossified but retain large areas of cartilage at the anterior and posterior tips (Fig. 16C) of the autopalatine, and within the hyomandibula, quadrate, and metapterygoid.

The main changes observed in specimens ranging between 24 and 29 mm length are the increase in the ossification, the loss of contact between the anterior cartilage of the autopalatine and the premaxilla, the enlargement of the membranous outgrowth of the hyomandibula, and the development of the levator arcus palatini crest (Fig. 16A—C).

In large specimens of *Diplomystes*, the autopalatine (Figs. 17A, B, 18A, 19A, B) is an elongate, somewhat sigmoidal bone that is more broad anteriorly than posteriorly. Anteriorly, this bone has two articular maxillary processes (Figs. 17B, 19A, B) that may fuse to produce a single elongate articular facet (Fig. 17C). When the two processes are separate, the lateral one is slightly broader than the medial one. The maxillary processes of the autopalatine articulate with two small processes of the maxilla that bear articular facets on the maxilla (Fig. 19B). The anterior fibrocartilage(s) of the autopalatine is lateral to the premaxilla. Dorsally, the autopalatine may have a crest ending in the ar-ticular process for the lateral ethmoid, which is dorsolateral. The vomerine process of the autopalatine is dorsomedial; it has an elongate, ovoid articular facet in *Diplomystes chilensis* (Fig. 17C), whereas the facet is comparatively smaller in *D. camposensis* (Fig. 17B).

The posterior part of the autopalatine (Figs. 17B, C, 18A) is elongate — longer than the anterior portion — in *Diplomystes camposensis*, and comparatively shorter in *D. chilensis* and *D. nahuelbutaensis*. The posterior part (Fig. 18A) is directed medially, and does not overlap the metapterygoid as it does in most siluroids (see below). The posterior fibrocartilage of the autopalatine is elongate and oval shaped and the en-topterygoid (when present) fits onto the posteroventral part of this fibrocartilage via connective tissue. I have not seen any ligaments uniting the posterior part of the autopalatine with the neurocranium.

The ectopterygoid (Figs. 19A, B) — when present — is a small, oval, thin, plate-like bone firmly attached by connective tissue to the posteroventral part of the autopalatine. The entopterygoid (Fig. 19A, B) is a cup-like bone partially surrounding the postero-ventral end of the autopalatine and in addition to the cup-like part, a small oval plate of thin bone extends posteriorly.

The metapterygoid (Figs. 17A, 18C) is strongly ossified and has a complex shape. The bone is markedly notched dorsally and ventrally, therefore it is broader at both ends than in the mid-section. The anterior portion projects medially as a sharp processus basalis, and projects laterally in a sharp, broad ectopterygoid process. This process oc-cupies the position of the ectopterygoid in other teleosts. Anteriorly, there is a short ligamentous connection between the ectopterygoid process and the autopalatine, and the processus basalis is connected by ligaments mainly to the vomer but also to the
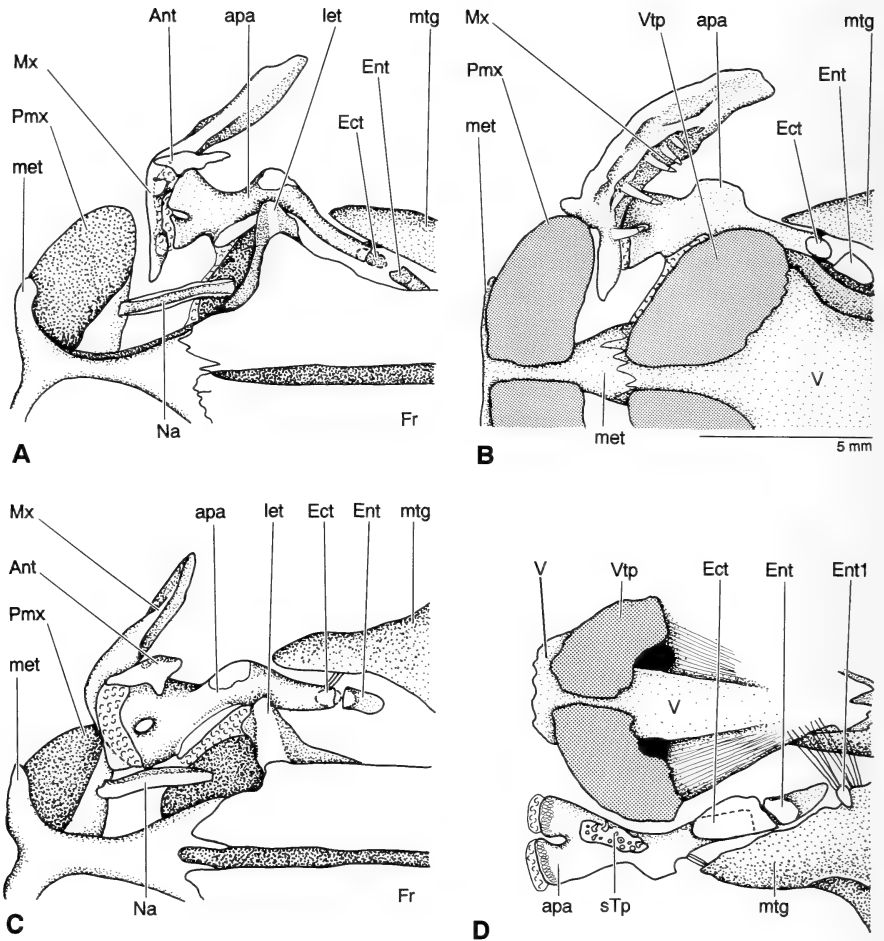
Fig.19: Autopalatine and surrounding bones in diplomystids. — A: *Diplomystes camposensis*, dorsal view; B: *D. camposensis*, ventral view; C: *Olivaichthys viedmensis*, dorsal view (FMNH 58004); D: *O. viedmensis*, ventral view (PC 20279). A—D, same scale.

Ant: antorbital; apa: autopalatine; Ect: ectopterygoid; Ent: entopterygoid; Ent1: 'entopterygoid' type 1; Fr: frontal; let: lateral ethmoid; met: mesethmoid; mtg: metapterygoid; Mx: maxilla; Na: nasal; Pmx: premaxilla; sTp: subautopalatine toothplate; V: vomer; Vtp: vomerine toothplate.

parasphenoid. Posteriorly, the metapterygoid is mainly sutured (sutura limbata) to the hyomandibula. However, it also synchondrally articulates with the quadrate and symplectic cartilage. In some large specimens the symplectic cartilage is almost gone. Grande (1987: 35) reported the presence of "what appears to be a large foramen" in the metapterygoid of one diplomystid specimen and in †*Hypsidoris*; I did not find this foramen in the diplomystid specimens I examined, but there are a variable number of
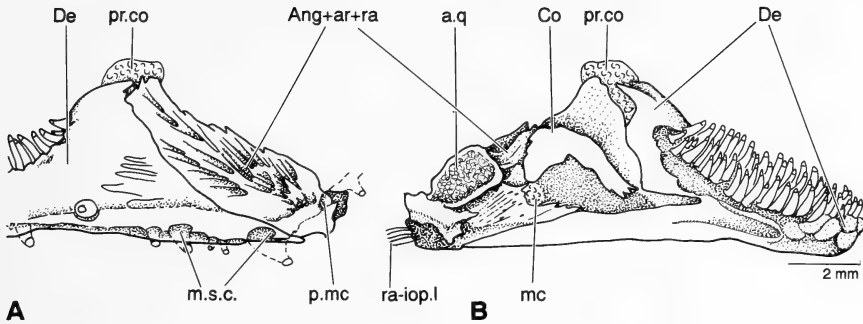
Fig.20: Lower jaw of *Diplomystes camposensis* (slightly modified from Arratia 1987a). — A: Posterior part, lateral view; B: Medial view.
Ang+ar+ra: angular, articular, and retroarticular fused; a.q: articular facet for quadrate; Co: coronomeckelian bone; De: dentary; mc: Meckelian cartilage; m.s.c.: mandibular sensory canal; p.mc: posterior opening of the mandibular sensory canal; pr.co: cartilaginous coronomeckelian process; ra-iop.l: retroarticular-interopercular ligament.

small foramina that may be present or completely absent within species. It seems likely then, that Grande simply described yet another variant.

The quadrate (Figs. 14A, B, 17A) is short, compact, and lacks the chondral or membranous pterygoid process described for other siluroids (Arratia 1990a), as well as the membranous posterior process present in other ostariophysans. Anteroventrally, the quadrate articulates through a slightly convex surface (it is not a true condyle) with the articular portion of the angulo-articulo-retroarticular (Fig. 20A, B; Arratia 1987a: Figs. 7A—C, 15A, C, 26A—F); however, an additional articular facet may be found in some large individuals (Arratia 1987a: Fig. 26E). Anterodorsally, the quadrate articulates through a short synchondral joint with the metapterygoid. Dorsally, the quadrate articulates with the hyomandibula through the symplectic cartilage and posteroventrally the quadrate is sutured with the preopercle.

In large specimens, the hyomandibula (Figs. 14A, B, 17A) is a broad, short bone whose anterior membranous outgrowth is large and well ossified. The dorsal margin of the membranous outgrowth of the hyomandibula forms the processus anterodorsalis which extensively articulates (bone-to-bone) with the pterosphenoid. This bone-to-bone articulation may be longer than the cartilaginous articular facet for the autosphenotic, prootic, and pterotic, resulting in a remarkably long syndesmotic joint between the processus anterodorsalis of the hyomandibula and the pterosphenoid. Arratia (1987a) considered this double articulation (diarthrosis and syndesmosis) of the hyomandibula with the pterosphenoid, sphenotic, prootic, and pterotic as an advanced feature of the Diplomystidae within the Siluroidei.

The hyomandibula articulates ventrally with a thick symplectic cartilage and anteriorly with the quadrate through a short dentate suture. The dentate suture is so short that it may be represented by only one or two indentations. The metapterygoid overlaps the hyomandibula through a wide lateral articulation over the anterior membranous out-

growth of the hyomandibula producing a lap joint or sutura limbata. Posteriorly, the hyomandibula articulates with the opercle through the opercular process, and the hyomandibula is sutured to the dorsal limb of the preopercle. On its medial face, the hyomandibula has a small area for the attachment of the first pharyngobranchial; the pseudobranch is almost vertical to the anterior membranous outgrowth.

The levator arcus palatini crest, horizontal to the lateral face of the hyomandibula, is well-developed in *Diplomystes chilensis* and *D. nahuelbutaensis*, whereas is rudimentary in *D. camposensis* (Arratia 1987a: Figs. 6B, 16, 25D). The development of the crest results in different patterns of exit of the hyoideomandibular nerve trunk (Fig. 21A, B) on the lateral surface of the bone. This nerve pierces the hyomandibula medially, and runs a short distance through the bone to exit just ventral to the levator arcus palatini
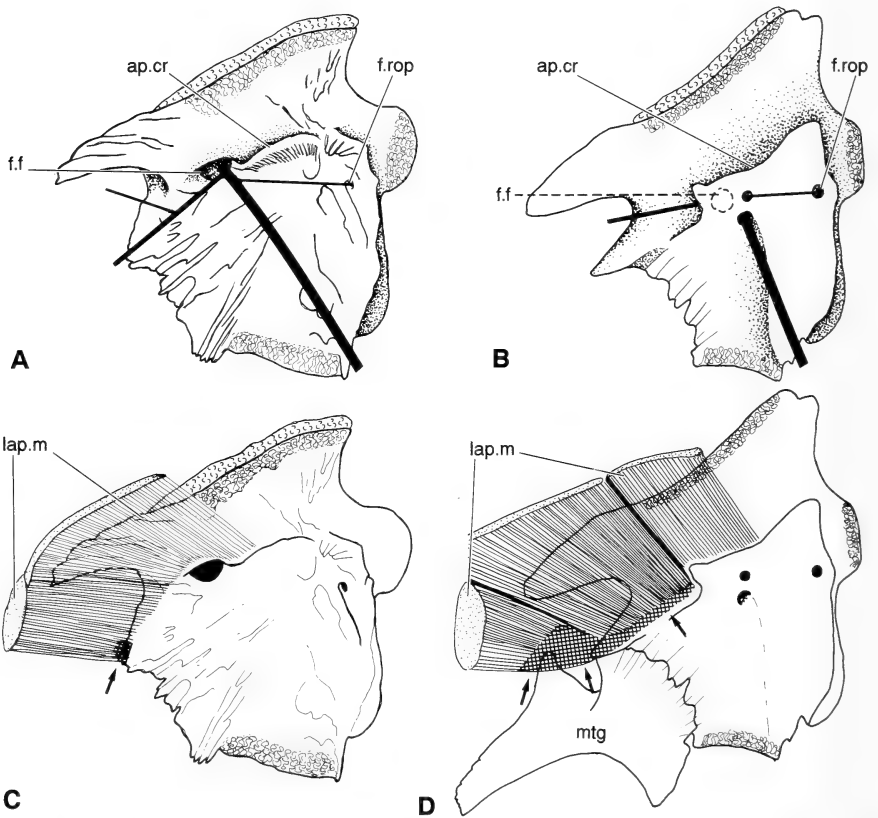
Fig.21: Hyoideomandibular nerve trunk and levator arcus palatini muscle and its tendinous attachment (indicated by arrows) in diplomystids. — A: Trajectory of the hyoideomandibular nerve trunk on the lateral aspect of hyomandibula in *Diplomystes camposensis* (after Arratia 1987a); B: Trajectory of the hyoideomandibular nerve trunk in *D. chilensis* (after Arratia 1987a); C: Levator arcus palatini muscle in *D. camposensis* (PC 220189); D: Levator arcus palatini muscle in *D. chilensis* (CAS-SU 13706).

ap.cr: levator arcus palatini crest; f.f: foramen for passage of hyoideomandibular nerve trunk; f.rop: foramen for ramus opercularis; lap.m: levator arcus palatini muscle; mtg: metapterygoid.

crest in *D. nahuelbutaensis*. It then branches into the ramus hyomandibularis, the ramus opercularis, and an anterior ramus that bifurcates into a small ramus innervating the levator arcus palatini muscle, and another ramus that runs anteriorly and may innervate the lateral portion of the eye and/or the skin. In *D. chilensis*, the facial nerve bifurcates inside the levator arcus palatini crest, therefore the ramus hyoideomandibularis and ramus opercularis have separate exits. In *D. camposensis*, the lateral opening of the hyoideomandibular nerve trunk is exposed, because the levator arcus palatini crest is rudimentary. The ramus opercularis runs posteriorly, pierces the hyomandibula and exits posteromedially to innervate the opercle. The hyoideomandibular nerve trunk runs laterally and may penetrate the hyomandibula at its posteroventral corner and exit medially, or it may just run through a small foramen between the hyomandibula, quadrate and preopercle.

In addition to the differences in the size of the levator arcus palatini crest and arcus palatini process, there are differences in the development of the levator arcus palatini muscle. In *Diplomystes camposensis*, which has a rudimentary crest and process, the muscle (Fig. 21C) is thin and has a small tendinous attachment to the levator arcus palatini process. The muscle inserts on the sphenotic and frontal, but not on the lateral ethmoid. In addition, the levator arcus palatini muscle of *D. camposensis* has two sections weakly distinguishable laterally. In contrast, three sections are observed in *D. chilensis* (Fig. 21D), the anteriormost one is well-developed, thick, and tendinously attached to the levator arcus palatini process of the hyomandibula and metapterygoid; the other two sections are thin and attached at the dorsal margin of the levator arcus palatini crest; the insertion of the muscle is similar to that of *D. camposensis*.

The suspensorium of *Olivaichthys viedmensis* has the same general pattern of that of *Diplomystes*. Some differences are as follows. The autopalatine of *Olivaichthys* bears one or two large articular fibrocartilage surfaces anteriorly that reach the posterolateral corner of the premaxilla (Fig. 19C, D); both bones are linked by a short piece of connective tissue. A small, flat, 'entopterygoid' type 1 is present anteromedial to the dorsomedial process of the metapterygoid in a single specimen. I have not observed a subautopalatine toothplate in young specimens, but in large specimens a patch (or patches) with conical teeth enlarges throughout growth (although it sometimes may be absent); this toothplate is not fused to the autopalatine. Only in one specimen of *Diplomystes chilensis* did Arratia (1987a: 24) observe a small subautopalatine toothplate with six conical teeth.

The ligamentous connections among the bones of the suspensorium of diplomystids may vary (Arratia 1987a: 26); nevertheless, the following ligaments are observed: there is a ligament connecting the quadrate, autopalatine, and maxilla as in other catfishes (see below) that in diplomystids joins the ligamentum primordiale and inserts broadly on the posteromedial face of the maxilla. The dorsomedial part of the processus basalis of the metapterygoid is linked through a broad ligament to the vomer (mainly) and also to the parasphenoid. A short ligament extends between the ectopterygoid process of the metapterygoid and the autopalatine (ligament 17 of Ghiot et al. 1984). The 'entopterygoid' type 1 — when present — lacks ligamentous connections with the lateral ethmoid,

orbitosphenoid, and autopalatine (Figs. 2A, 19D); but is linked to the vomer. Anteriorly, the autopalatine is joined by short ligaments and/or connective tissue to the antorbital laterally and lateral ethmoid medially. In its middle region, the autopalatine is ligamentously linked to the metapterygoid and quadrate, and posteriorly to the orbitosphenoid.
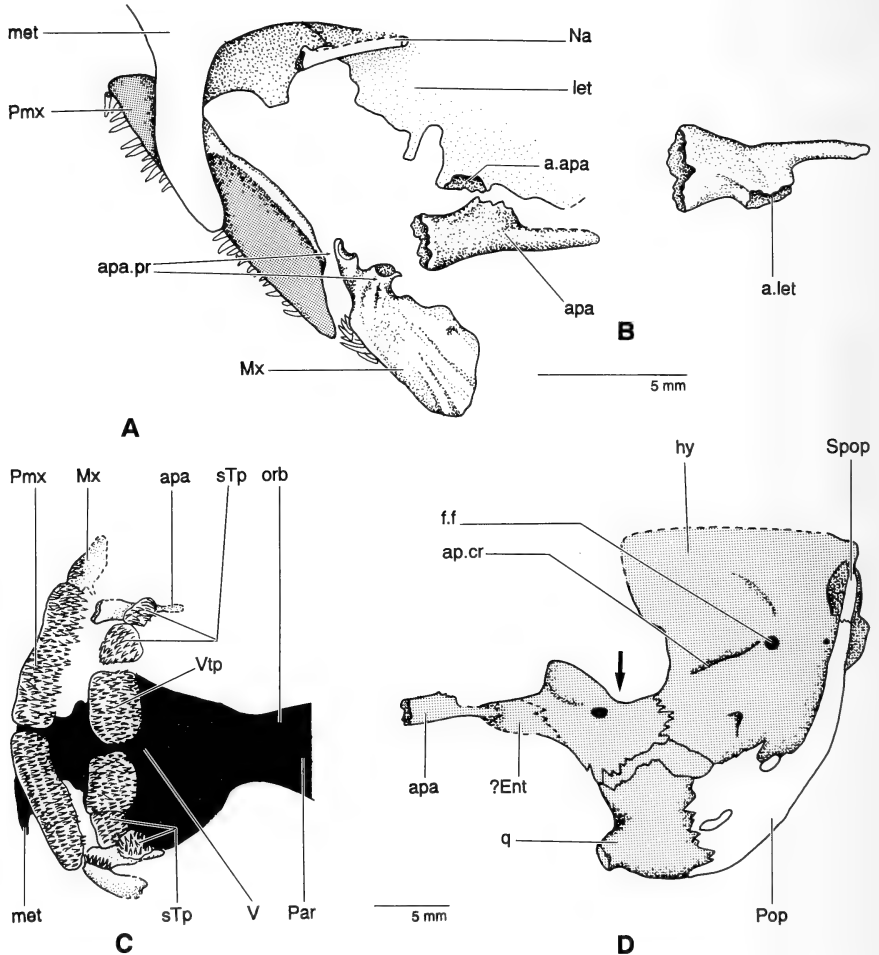
Fig.22: Suspensorium of †*Hypsidoris farsonensis* (after Grande 1987). — A: Dorsal view of autopalatine, maxilla, and premaxilla; B: Dorsal view of the autopalatine; C: Autopalatine and surrounding bones, ventral view; D: Restoration of the suspensorium, lateral view. Arrow points to a notch.
a.apa: articular facet for autopalatine; a.let: articular facet for lateral ethmoid; apa: autopalatine; apa.pr: autopalatinal process; ap.cr: levator arcus palatini crest; ?Ent: ?entopterygoid; hy: hyomandibula; let: lateral ethmoid; met: mesethmoid; Mx: maxilla; Na: nasal; orb: orbitosphenoid; Par: parasphenoid; Pop: preopercle; Pmx: premaxilla; q: quadrate; Spop: suprapreopercle; sTp: subautopalatine toothplate; V: vomer; Vtp: vomerine toothplate.

†Hypsidorids

The description of the suspensorium of †*Hypsidoris farsonensis* from the Eocene of the Green River Formation is based on Grande's (1987) reconstruction and my reinterpretation of some of his characters.

The autopalatine (Fig. 22A, B) is expanded anteriorly to probably form two articular facets for articulation with the two facets of the maxilla. Although the double articulation between the maxilla and autopalatine is also present in diplomystids (compare Figs. 18A, B, 19A—C, 22A), †*Hypsidoris* lacks the long anterior maxillary process that completely separates the autopalatine from the premaxilla in diplomystids. The autopalatine of †*Hypsidoris* (Fig. 22C), like that of *Olivaichthys*, may have reached the posterolateral corner of the premaxilla. The posterior part of the autopalatine — unlike that of diplomystids and nematogenyids — seems to be dorsal to the entopterygoid (Fig. 22D) and not medial to the metapterygoid. Grande (1987: Fig. 4) illustrated the autopalatine as bearing an articular facet for the lateral ethmoid; it is unknown though, whether the autopalatine of †*Hypsidoris* also articulated with the vomer. Two small subautopalatine toothplates (named as accessory ectopterygoid toothplates by Grande 1987) are present. One is ventral to the autopalatine, the second is between the ventral part of autopalatine and the lateral margin of the vomer (Fig. 22C).

A small, slightly elongate entopterygoid is present. The entopterygoid has been interpreted by Grande (1987) as probably being sutured with the metapterygoid. This condition is unlikely, when you compare it with other primitive siluroids. In large ictalurids and some pimelodids (see below) the entopterygoid and metapterygoid may be close to each other and become indented or serrated, but they are linked to each other by a ligament. With the available information, I am unable to establish whether this entopterygoid is a dermal or a sesamoid pterygoid as found in extant siluroids above the level of the Diplomystidae.

Grande (1987) could not find an ectopterygoid in †*Hypsidoris* and he expected that it could be hidden by other bones. I hypothesize that †*Hypsidoris* does not have an ectopterygoid.

The metapterygoid (Fig. 22D) is a slightly rectangular bone which bears a pronounced processus basalis that is separated by a deep notch from the posterodorsal part of the bone as in diplomystids, but it is missing the ectopterygoid process found in diplomystids and other primitive siluroids (compare Figs. 17A, 19C, 22D). Another possibility is that the bone labelled by Grande (1987) as the entopterygoid, is really the broken ectopterygoid process of the metapterygoid.

It is unclear whether †*Hypsidoris* has a simple or complex quadrate, because small individuals have not been studied. The quadrate of †*Hypsidoris* is similar in shape to that of adult *Pylodictis*; although the quadrate of *Pylodictis* develops a small projection anteriorly during ontogeny, the origin of the bone is similar to the simple quadrate in diplomystids, ictalurids, and nematogenyids. With the available information, I therefore hypothesize that †*Hypsidoris* has a simple quadrate.
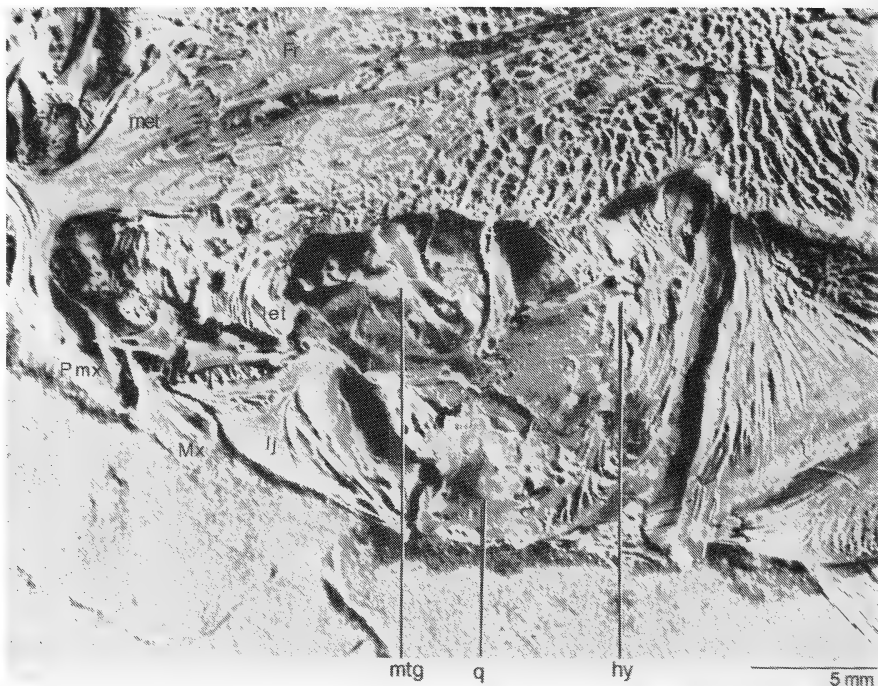
Fig.23: Head of †*Hypsidoris farsonensis*, dorsolateral view (Peel of holotype PU 20570a).
Fr: frontal; hy: hyomandibula; let: lateral ethmoid; lj: lower jaw; met: mesethmoid; mtg: metapterygoid; Mx: maxilla; Pmx: premaxilla; q: quadrate.

The large hyomandibula (Figs. 22D, 23) is incompletely known; its dorsal margin is covered by other bones in specimens studied by Grande (1987). The levator arcus palatini crest is smaller than in diplomystids and closer to the anteroventral portion of the bone than the dorsal portion (compare Figs. 14B, 21A, B, 22D). The facial nerve runs through a canal inside the bone according to Grande's restoration (1987). This would be different than diplomystids (compare Figs. 21A, B, 22D), and is remarkably curious because there is a visible lateral foramen for the facial nerve in the hyomandibula.

Ictalurids

The development of the suspensorium of catfishes with a simple quadrate is based on a detailed description of *Ictalurus punctatus*. The series of *I. punctatus* examined included 146 cleared and stained specimens, ranging from 6 mm total length through 65 mm standard length, in addition to numerous large individuals prepared as dry skeletons and cleared and stained material.

In 6 mm total length specimens (one day after hatching), the elements of the suspensorium (Fig. 24A) as well as those of the branchial arches are cartilaginous. The pars autopalatina is a large plate of cartilage bearing the maxillary barbel laterally. The max-

illary barbel is not preformed in hyaline cartilage, and the position and distribution of its cellular elements differs from the cartilaginous areas of the suspensorium. The pars autopalatina and the hyo-symplectic-pterygoquadrate plate are broadly separated from each other. The hyo-symplectic-pterygoquadrate plate is synchondrotic with the ventral portion of the hyoid arch, as well as the Meckelian cartilage, and the endocranium. The
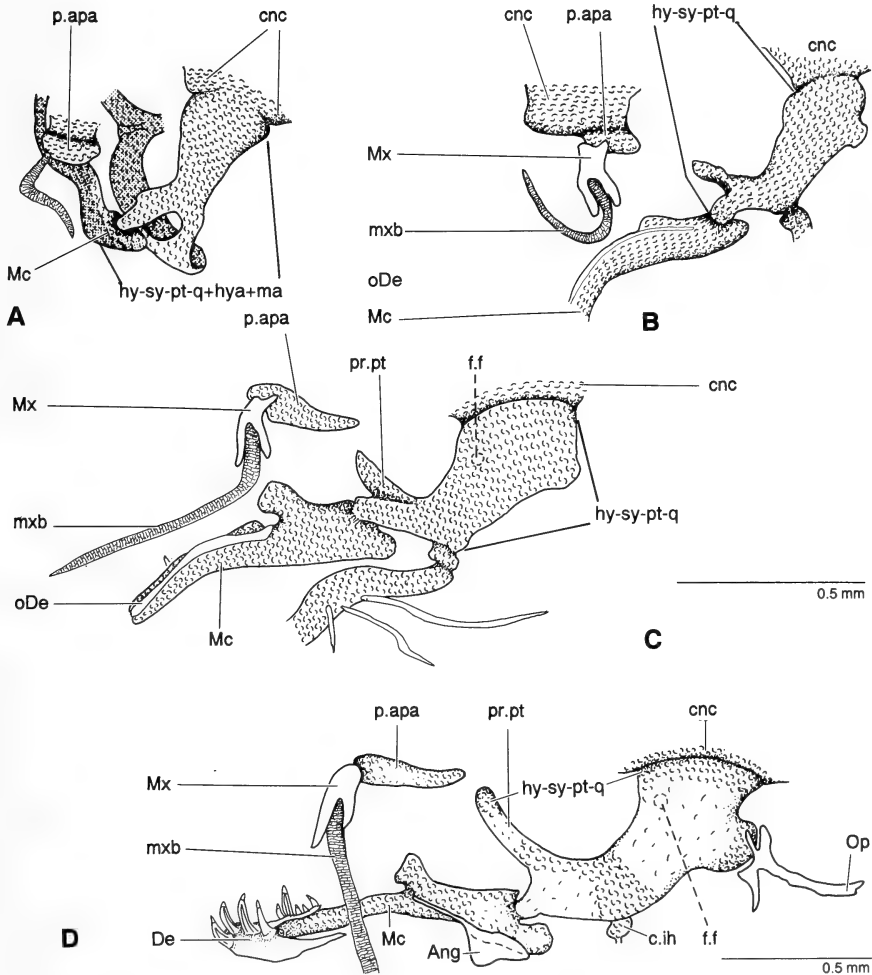
Fig.24: Sequence of the development of the suspensorium in *Ictalurus punctatus*, lateral view (KU uncat.). — A: 6 mm total length; B: 7 mm total length; C: 8.5 mm total length; D: 9 mm total length. A—C same scale. Ang: angular; De: dentary; c.ih: cartilaginous interhyal; cnc: cartilaginous neurocranium; f.f: foramen for passage of hyoideomandibular nerve trunk; hy-sy-pt-q: hyo-symplectic-pterygoquadrate plate; hy-sy-pt-q+hya+ma; hyo-symplectic-pterygoquadrate plate synchondrotic with the ventral limb of hyoid arch and mandibular arch; mc: Meckelian cartilage; Mx: maxilla; mxb: maxillary barbel; oDe: ossification center of dentary; Op: opercle; p.apa: pars autopalatina; pr.pt: processus pterygoideus.

hyo-symplectic-pterygoquadrate plate has a short anterior cartilaginous pterygoid process.

In 7 mm total length specimens (two days after hatching), a well ossified, small maxilla (Fig. 24B) articulates laterally with the pars autopalatina; the maxillary barbel is associated with the maxilla. There are changes in the cartilage of the areas where the articulation for quadrate and articular bone and hyomandibula and interhyal will form; there is a small cartilaginous opercular process in the dorsoposterior margin of the hyo-symplectic-pterygoquadrate plate and the pterygoid process is more elongate. Still the Meckelian cartilage forms one unit anteriorly, but it is not synchondrotic with the hyoid arch as it is in trichomycterids (Arratia & Schultze 1990: Fig. 15A—D). At this stage, the Meckelian cartilage develops a dorsal process which I identified as the coronoid cartilage in diplomystids (Arratia 1987a); there is a long, thin, and narrow dermal ossification above and lateral to the Meckelian cartilage; this corresponds to the dentary.

In 8.5 to 9 mm total length (3 or 4 days after hatching), the anterior part of the elongate pars autopalatina (Fig. 24A, B) has expanded medially and lies ventral to the endocranium, in the region where the future lateral ethmoid will form. At this stage, the pars autopalatina appears synchondrotic with the ethmoidal region in some specimens, whereas both parts are separate in other specimens (Fig. 24C—D). The main changes are the growth of the pars autopalatina and pars pterygoquadrata, resulting in these elements becoming closer. The coronoid process of the Meckelian cartilage enlarges considerably, as does the dentary (which bears one or a few teeth). Three slender, ossified, branchiostegal rays are associated with the cartilaginous ventral portion of the hyoid arch.

In 10 to 10.5 mm total length (5 days after hatching) there are significant changes in the structure of the hyo-symplectic-pterygoquadrate plate. Although only a single cartilaginous element is observed, the regions of the future metapterygoid, hyomandibula, and quadrate (Fig. 25A) are identifiable because of the change in density of the cartilaginous cells. This change in density is also true of the future articular bone in the Meckelian cartilage. The pars autopalatina and pars pterygoquadrata continue their elongation and become closer to each other. The pars autopalatina is separate from the ethmoidal cartilage. Similarly, the hyomandibular region is separate from the endocranial cartilage. There is complete separation between the pars pterygoquadrata and the Meckelian cartilage, and between the interhyal cartilage and the hyo-symplectic-pterygoquadrate plate. The retroarticular begins to ossify at the posterior margin of the Meckelian cartilage; the symphyseal articulation separating the Meckelian cartilage into left and right elements is formed. The dentary enlarges considerably, to produce two processes posteriorly, the coronoid process and the long posteroventral process, which is closer to the retroarticular.

In 11.7—12 mm standard length (7 days after hatching) the main change is the beginning of the ossification of the autopalatine. A small 'entopterygoid' appears between 12 and 13 mm standard length (about 9 days after hatching). The bone begins to form in the rod of connective tissue that links the metapterygoid, lateral ethmoid, vomer, and autopalatine. At this stage, the hyomandibula and quadrate begin to be finely,

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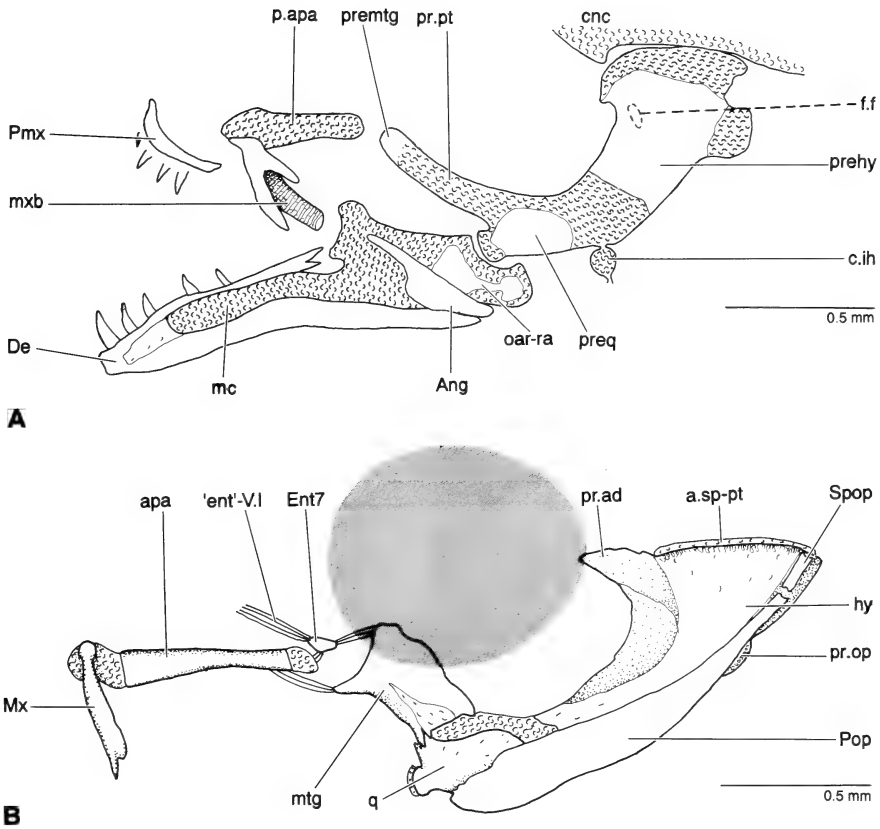
Fig.25: Suspensorium of *Ictalurus punctatus*, lateral view (KU uncat.) and position of eye (dotted area). — A: 10 mm standard length; B: 54 mm standard length.
Ang: angular; apa: autopalatine; a.sp-pt: articular facet for sphenotic and pterotic; c.ih: cartilaginous interhyal; cnc: cartilaginous neurocranium; De: dentary; Ent7: 'entopterygoid' type 7; 'ent'-V.l: 'entopterygoid'-vomer ligament; f.f: foramen for passage of hyoideomandibular nerve trunk; hy: hyomandibula; mc: Meckelian cartilage; mtg: metapterygoid; Mx: maxilla; mxb: maxillary barbel; oar-ra: ossification center of articular and retroarticular; p.apa: pars autopalatina; prehy: preformed hyomandibula; premtg: preformed metapterygoid; preq: preformed quadrate; Pmx: premaxilla; Pop: preopercle; pr.ad: processus anterodorsalis; pr.op: processus opercularis; pr. pt: processus pterygoideus; q: quadrate; Spop: suprapreopercle.

perichondrally ossified. Between 14 and 15.5 mm standard length all of the bones of the suspensorium are ossified despite the presence of large cartilaginous areas between them. From this stage on, the main changes are related to the ossification of the bones, and the appearance of ligaments replacing the connective tissue between 'entopterygoid' and metapterygoid, the 'entopterygoid' and the lateral ethmoid (ligament 2 of Ghiot et al. 1984), the 'entopterygoid' and the vomer, and 'entopterygoid' and autopalatine. In addition, the metapterygoid is linked to the lateral ethmoid (ligament 18 of Ghiot et al. 1984).
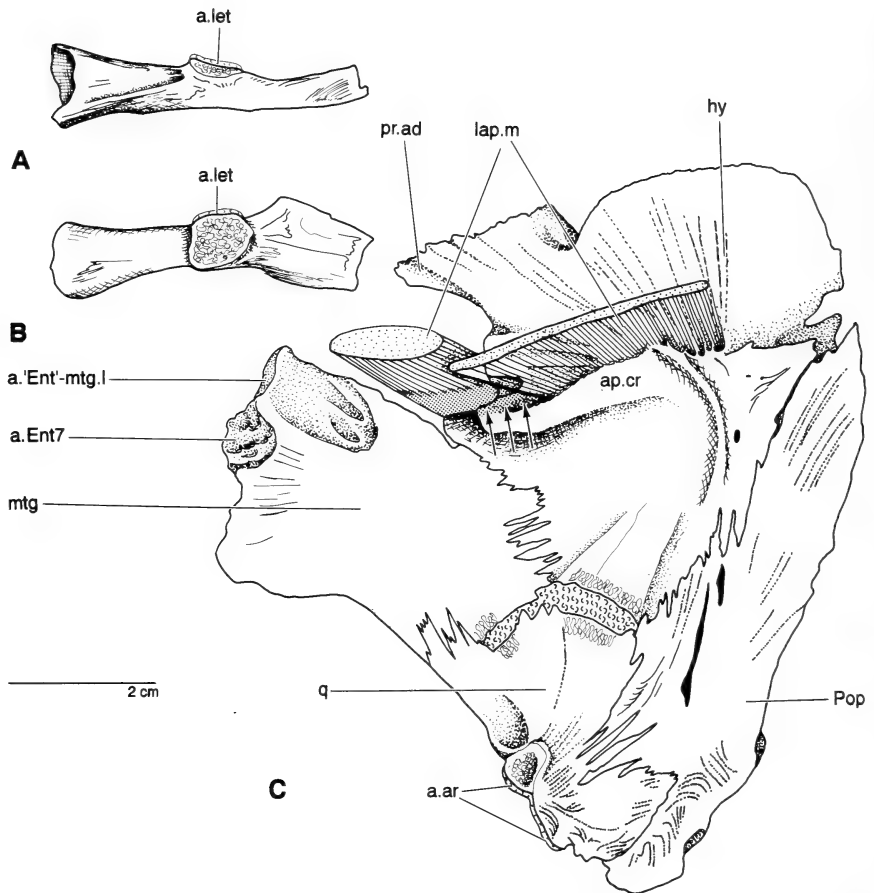
Fig.26: Suspensorium of *Ictalurus punctatus* (KU 21429). — A: Autopalatine, left side, dorsal view; B: Autopalatine, medial view; C: Posterior part of the suspensorium, levator arcus palatini muscle and its tendinous area (indicated by arrows), and preopercle.
a. ar: articular facet for articular; a.Ent7: sutural surface for 'entopterygoid' type 7; a.'Ent'-mtg.l: attachment surface for 'entopterygoid'-metapterygoid ligament; a.let: articular facet for lateral ethmoid; ap.cr: levator arcus palatini crest; hy: hyomandibula: lap.m: levator arcus palatini muscle; mtg: metapterygoid; Pop: preopercle; pr.ad: processus anterodorsalis; q: quadrate.

In specimens of about 50 mm length and larger (Figs. 25B, 26A—C) the autopalatine — which is rod-like — articulates with the lateral ethmoid. The 'entopterygoid' enlarges and gets closer to the metapterygoid; such that both bones may suture during growth. The arcus palatini process of the hyomandibula is well ossified and large. The levator arcus palatini muscle, divided into two sections of different sizes, attaches to the process and the levator arcus palatini crest; and this muscle inserts onto the autosphenotic and frontal.

The anterior part of the suspensorium in ictalurids has interesting differences between species. The highest number of ligamentous connections of the 'entopterygoid' is found
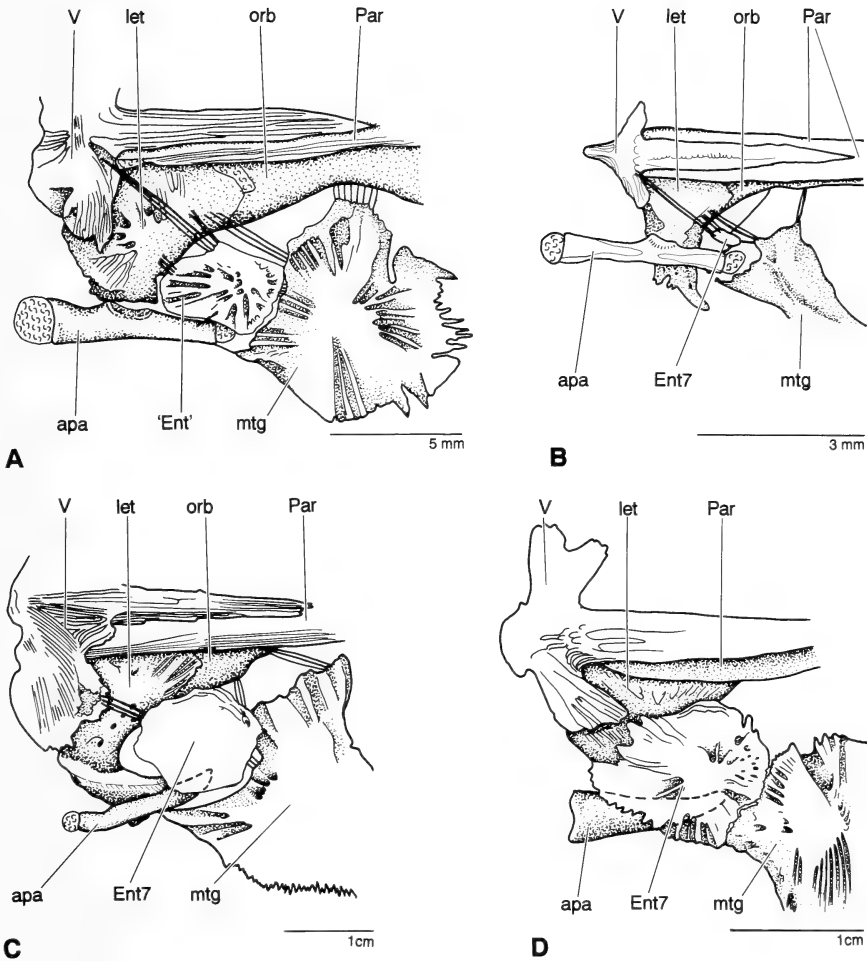
Fig.27: Anterior part of the suspensorium in ventral view of some ictalurids. — A: *Ameiurus melas* (135 mm standard length; KU 103843); B: *Ictalurus punctatus* (59 mm standard length; KU 9657); C: *Pylodictis olivaris* (KU 1746, KU 10414, and KU 15697); D: *Ictalurus furcatus* (81 mm standard length; KU 21381); ligaments omitted.
apa: autopalatine; 'Ent': 'entopterygoid'; Ent7: 'entopterygoid' type 7; let: lateral ethmoid; mtg: metapterygoid; orb: orbitosphenoid; Par: parasphenoid; V: vomer.

in *Ameiurus melas* (Fig. 27A); a high number is also found within the ictalurids (type 7). An 'entopterygoid' is missing in *Prietella* (Lundberg 1982). The 'entopterygoid' is in close contact with the metapterygoid, vomer, and lateral ethmoid in some individuals of *Ictalurus* and *Pylodictis*; it may even be sutured to the metapterygoid and vomer in large specimens. Another difference is that in *Ameiurus, Ictalurus,* and *Pylodictis* (Fig. 27A—C), the autopalatine does not extend dorsal to the metapterygoid, but only dorsal to the 'entopterygoid'; whereas in *Noturus* the autopalatine extends dor-

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sal to the metapterygoid — the condition commonly found in siluroids (see below). A well-developed lateral process is lateral to the metapterygoid in *Pylodictis* and some species of *Ictalurus*; in these species, the levator arcus palatini muscle also attaches on the lateral process of the metapterygoid.
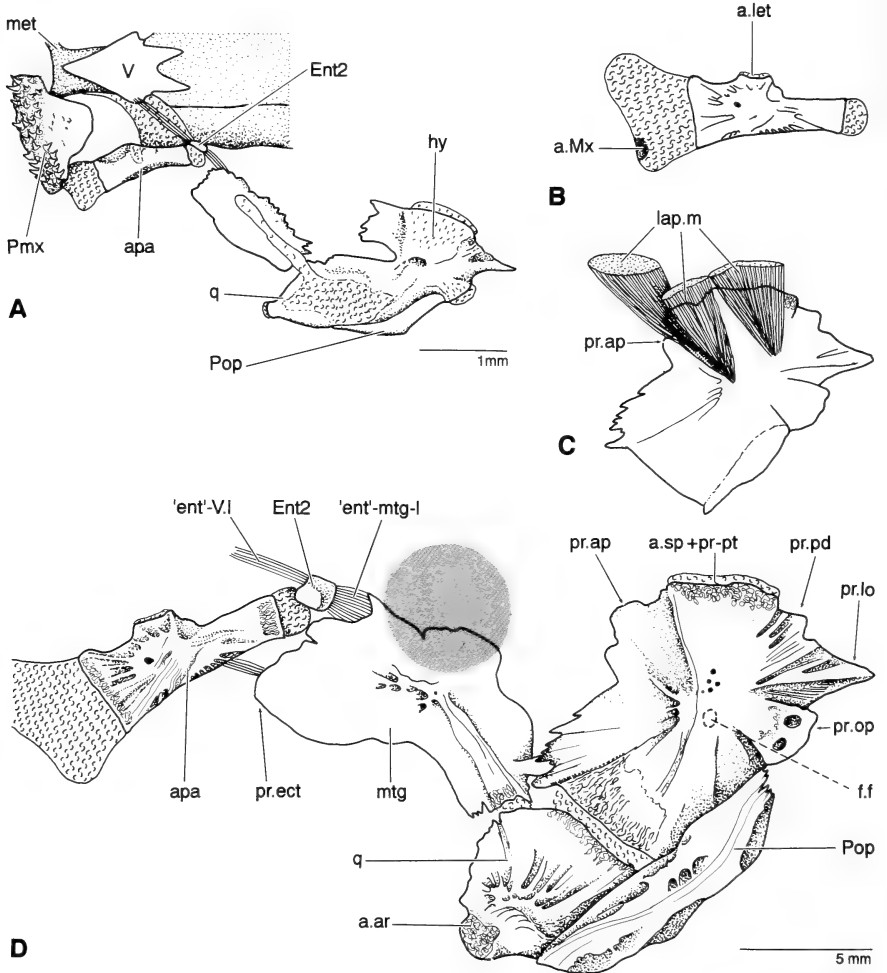
Fig.28: Suspensorium of *Nematogenys inermis*; dotted area represents the position of eye. — A: Suspensorium, ventral view (31.8 mm standard length; PC 131); B: Autopalatine, left side, dorsal view (about 200 mm; PC 30873); C: Insertion of levator arcus palatini muscle on lateral aspect of hyomandibula; D: Suspensorium, lateral view (about 200 mm; PC 30873). B—D same scale.

a. ar: articular facet for articular; a.let: articular facet for lateral ethmoid; a.Mx: articular facet for maxilla; apa: autopalatine; a.sp+pr-pt: articular facet for sphenotic+prootic and pterotic; Ent2: 'entopterygoid' type 2; 'ent'-mtg-l: 'entopterygoid'-metapterygoid ligament; 'ent'-V.l: 'entopterygoid'-vomer ligament; f.f: foramen for passage of hyoideomandibular nerve trunk; lap.m: levator arcus palatini muscle; met: mesethmoid; mtg: metapterygoid; Pmx: premaxilla; pr.ap: processus anterodorsalis; pr.ect: processus ectopterygoideus; Pop: preopercle; pr. lo: processus levator operculi; pr.op: processus opercularis; pr.pd: processus posterodorsalis; q: quadrate.

Nematogenyids

General information on the suspensorium of *Nematogenys inermis* may be found in Arratia (1990a: 207); here I will provide additional information.

The elements of the suspensorium form similarly to those of *Ictalurus*, but the position and size of bones of the suspensorium and cranium vary.

The autopalatine (Figs. 28A, D, 29A, B) is broader anteriorly than posteriorly, similar to the condition present in diplomystids and †*Hypsidoris*. The anterior cartilage of the autopalatine is large and lies in a dorsolateral cavity of the premaxilla. Laterally, the small maxilla articulates through two small articular processes with the anterior cartilage. At about half of the length of the autopalatine is an elongate articular facet for the lateral ethmoid and vomer; there is a direct articulation between the autopalatine and lateral ethmoid, and an indirect articulation via cartilage with the vomer. There is a mass of fibrocartilage at the posterior end of the autopalatine; it is closely attached by connective tissue with a small cup-like sesamoid bone, the 'entopterygoid' type 2. This 'entopterygoid' is connected by a short ligament to the metapterygoid, and by a long ligament to the vomer. Neither an ectopterygoid or an 'ectopterygoid' are present.

The metapterygoid forms similarly to that of diplomystids and *Ictalurus* (compare Figs. 16A—C, 25A, B, 28A). The metapterygoid (Fig. 28A, D) is the largest element of the palatoquadrate; dorsally it has a small notch separating the anterior region from the posterior one. The anterior region produces a sharp, short processus basalis. Ventro-
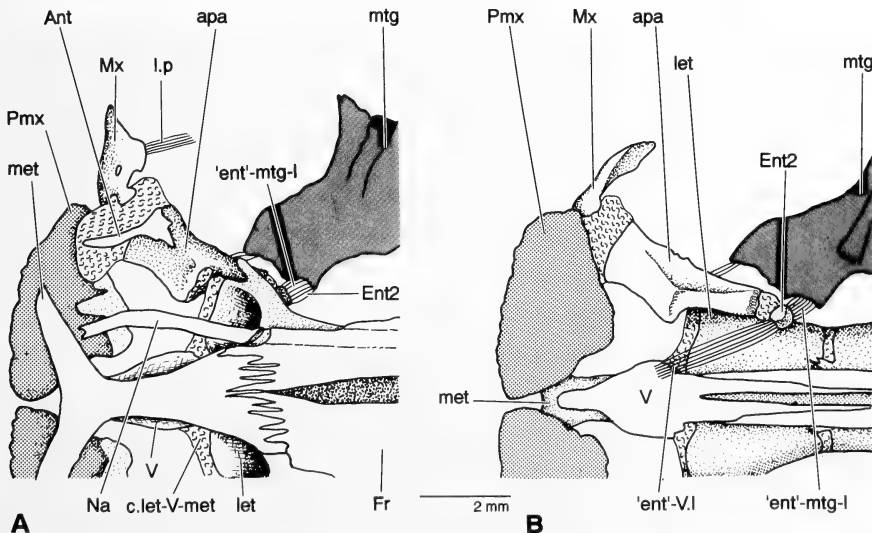
Fig.29: Autopalatine and surrounding bones in *Nematogenys inermis* (PC 30873). — A: Dorsal view; B: Ventral view; A,B same scale.
Ant: antorbital; apa: autopalatine; c.let-V-met: cartilage joining lateral ethmoid, vomer, and mesethmoid; Ent2: 'entopterygoid' type 2; 'ent'-mtg.l: 'entopterygoid'-metapterygoid ligament; 'ent'-V.l: 'entopterygoid'-vomer ligament; Fr: frontal; let: lateral ethmoid; l.p: ligamentum primordiale; met: mesethmoid; mtg: metapterygoid; Mx: maxilla; Na: nasal; Pmx: premaxilla; V: vomer.

anteriorly, the metapterygoid projects a broad ectopterygoid process, that is lateral to the posterior portion of the autopalatine. The metapterygoid is loosely sutured with the hyomandibula. Most of the metapterygoid is membranous bone; the chondral region is elongate, narrow, and lies posteroventrally. There is an articulation between this chondral portion of the metapterygoid and the cartilaginous symplectic region between the hyomandibula and quadrate that is lost in some adult specimens. The suture between the metapterygoid and quadrate is not present, unlike other primitive siluroids. In addition, *Nematogenys* lacks a suture between the hyomandibula and quadrate.

The simple quadrate is a small bone, but a little larger than that in diplomystids. It bears large articular facets for the hyomandibula, preopercle, and the articular portion of the fused angulo-articulo-retroarticular (Fig. 30A, B). The main elements of this fusion of the angulo-articulo-retroarticular are the chondral ones; the angular is only a small ossification that may never contact the retroarticular portion of the Meckelian cartilage.

The hyomandibula has a moderately large, anterior, membranous outgrowth. Posterodorsally, there is a sharp elongate process — the processus levator operculi — just dorsal to the opercular process. A horizontal levator arcus palatini crest is not present, but a nearly vertical ridge for attachment of the levator arcus palatini muscle is present. The levator arcus palatini muscle (Fig. 28C) is subdivided into three portions. The largest or anterior one extends from the small levator arcus palatini process to the frontal, staying well separate from the lateral ethmoid; the other two portions are thin and extend from the lateral aspect of the hyomandibula to the autosphenotic.

The posteroventral margin of the hyomandibula is sutured to the preopercle. The dorsal margin of the hyomandibula articulates synchondrally with the pterotic and sphenotic + prootic. The pterosphenoid is not included in this cranial fusion as it was in trichomycterids. A small pseudobranch, with a few branchial lamellae, is associated with the medial aspect of the hyomandibula. The first pharyngobranchial is missing,
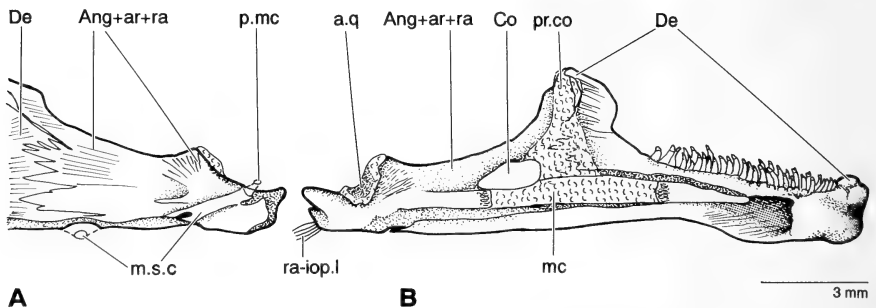
Fig.30: Lower jaw in *Nematogenys inermis* (PC 30873). — A: Posterior part, lateral view; B: Medial view. Ang + ar + ra: angular, articular and retroarticular fused; a.q: articular facet for quadrate; Co: coronomeckelian bone; De: dentary; mc: Meckelian cartilage; m.s.c.: mandibular sensory canal; p.mc: posterior opening of the mandibular sensory canal; pr.co: cartilaginous coronomeckelian process; ra-iop.l: retroarticular- interopercular ligament.

therefore there is no lateral attachment of this element to the hyomandibula like in diplomystids.
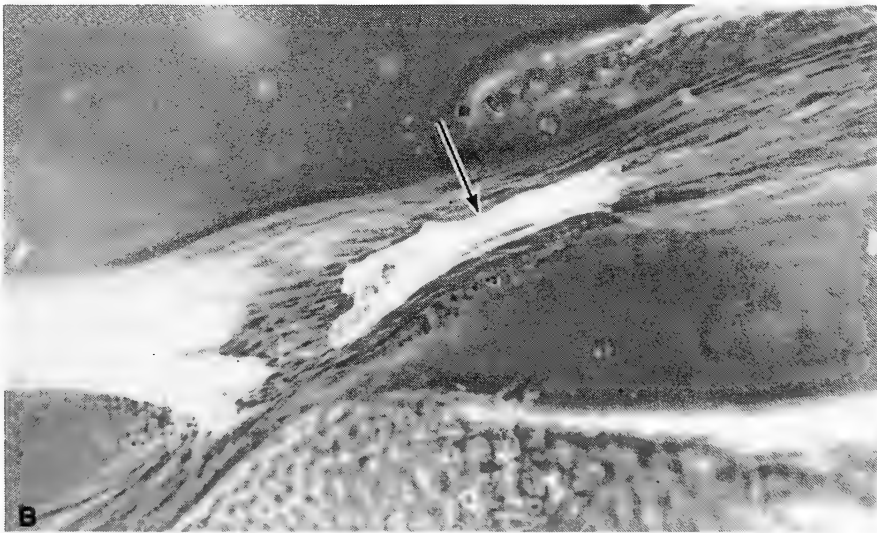
Fig.31: Suspensorium of *Noturus*. — A: *N. hildebrandi*, lateral view (5.5 mm total length; KU uncat.). Arrows point to the hyo-symplectic-pterygoid plate plus Meckelian cartilage; B: *Noturus exilis* (14 mm standard length; KU 17229). Arrows point to the 'entopterygoid' chalcifying in the ligament.

The ramus hyoideomandibularis of the facial nerve medially penetrates the hyomandibula and passes through a short tube inside the bone, emerging at the ventrolateral corner of the bone, as in ictalurids and most catfishes.

Ariids

The pterygoid series of *Bagre* and *Galeichthys* differs from those above described for catfishes with a simple quadrate. The small 'ectopterygoid' forms as an ossification in the ligament extending between the 'entopterygoid' and autopalatine; the the ligament becomes separated into two short ligaments, one between the 'entopterygoid' and 'ectopterygoid' and another between the 'ectopterygoid' and autopalatine. The small 'entopterygoid' is connected by ligaments and/or connective tissue with the lateral ethmoid, vomer, and metapterygoid.

Siluroids with a complex quadrate

Ictalurids

The two series of *Noturus* examined include 12 cleared and stained specimens of *Noturus hildebrandi* between 5.5 mm total length and 12.5 mm standard length, and 61 specimens of *Noturus exilis* ranging between 13.6 and 78 mm standard length. There are no major differences in the development of the suspensorium and hyoid arch between *Trichomycterus* (Arratia 1990a) and *Noturus*; however, the minor differences are of interest. In general, these differences are in the speed of ossification and the appearance of dermal elements as correlated with age (and represented by length).

In 5.5 mm specimens of *Noturus hildebrandi*, the hyoid and mandibular arches (Fig. 31A) are synchondrotic. The 'articulation' between the Meckelian cartilage and pars quadrata is produced by a fold of the cartilage. The only ossified bone at this stage is the cleithrum.

In 13.6 mm specimens of *Noturus exilis* the hyomandibular-symplectic-pterygoquadrate plate, the hyoid arch, and the pars autopalatina (Fig. 32A) are partially perichondrally ossified. The sesamoid 'entopterygoid' type 4 (anteriorly adjacent to the metapterygoid) is already ossified in the ligament linking the metapterygoid and vomer (Fig. 31B). There is no evidence that this 'entopterygoid' is the result of a fracture of the metapterygoid as suggested by Gosline (1975). The hyo-symplectic-pterygoquadrate plate is partially separated from the cranium. The anterior, membranous outgrowth of the hyomandibula is large. The quadrate complex is perichondrally ossified at the condylar region; anteriorly it also has a small membranous ossification. The metapterygoid has a thin, flat, membranous process (the ectopterygo-quadrate process) that is posterolateral to the autopalatine, occupying the position of the ectopterygoid in other teleosts. No lateral metapterygoid process was observed. The autopalatine is long and narrow. It is largely cartilaginous anteriorly, whereas the mid-section of the posterior part is partially surrounded by a fine perichondral ossification. The articular facet for the lateral ethmoid is about midway along the length of the bone. A ligament connects the posterior part of the autopalatine to the anterodorsal part of the metapterygoid.

The process of ossification then progresses and no major changes are observed in larger specimens. For example, in 16.1 mm specimens, changes in the density of the cartilage are observed in those regions that will later become synchondral articulations. The hyomandibula is largely ossified and articulates with the neurocranium. The metaptery-
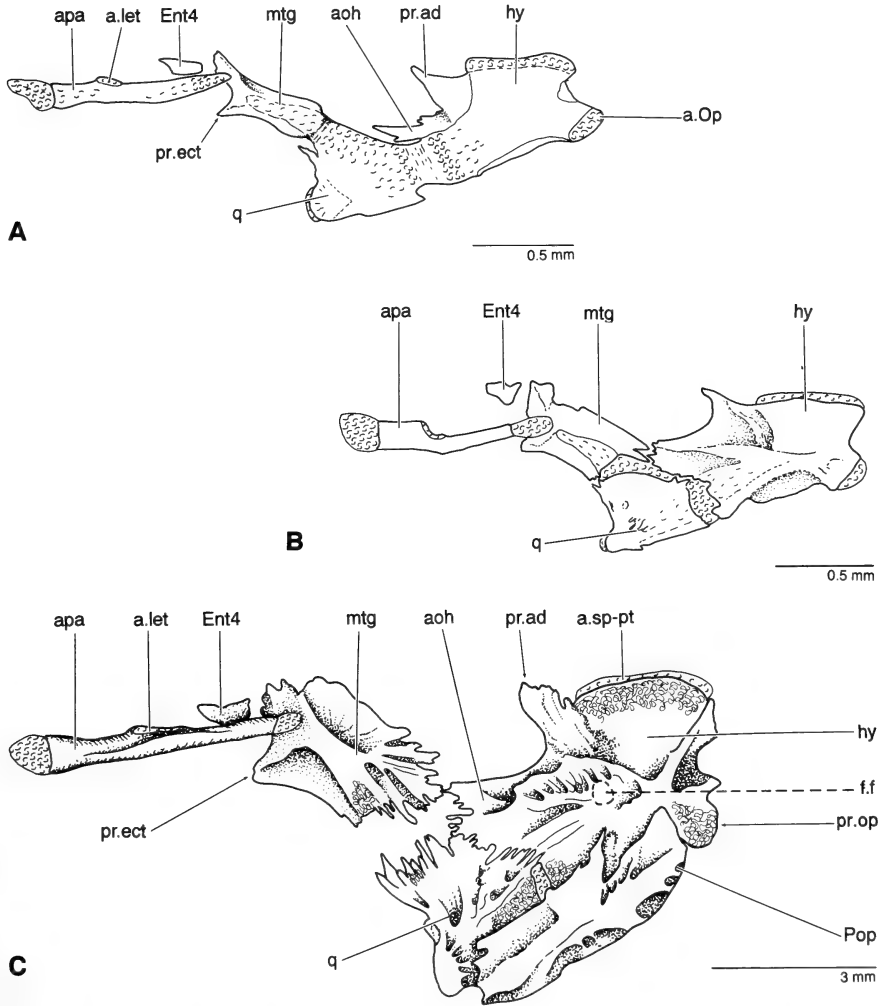
Fig.32: Developmental sequence of the suspensorium of *Noturus exilis*, lateral view (KU 17229). Ligaments omitted. — A: 13.6 mm standard length; B: 26.7 mm standard length; C: 73.9 mm standard length; the metapterygoid is slightly displaced dorsally to show its sutural and synchondral surfaces.
a.let: articular facet for lateral ethmoid; aoh: anterior membranous outgrowth; a.Op: articular facet for opercle; apa: autopalatine; a.sp-pt: articular facet for sphenotic and pterotic; Ent4: 'entopterygoid' type 4; f.f: foramen for passage of hyoideomandibular nerve trunk; hy: hyomandibula; mtg: metapterygoid; Pop: preopercle; pr.ad: processus anterodorsalis; pr.ect: processus ectopterygoideus; pr. op: processus opercularis; q: quadrate.

goid produces a posterodorsal process that faces the anterior membranous outgrowth of the hyomandibula.

In specimens of about 27 mm, the membranous regions of hyomandibula, complex quadrate, and metapterygoid (Fig. 32B) continue to enlarge. In 40—50 mm specimens, cartilaginous regions are only found between the hyomandibula and quadrate, and between the quadrate and metapterygoid. The metapterygoid enlarges dorsally and laterally through membranous projections or processes; its posterodorsal process produces serrations which articulate (sutura serrata) with the anterior membranous outgrowth of the hyomandibula, and just barely with the quadrate. The 'entopterygoid' type 4 does not change markedly in shape or relationships throughout ontogeny.

The changes observed in specimens of 50—74 mm are the enlargement of the sutural regions between the anterior membranous outgrowth of the hyomandibula, the dorsal region of the quadrate and the posterodorsal process of the metapterygoid (Fig. 32C). The autopalatine becomes mostly ossified, although the anterior region retains a large nodule of cartilage and the posterior region has a smaller cartilage.

In 78 mm specimens the anterior part of the autopalatine has a large, oval or round cartilage. The two articular facets of the maxilla articulate with this nodule of cartilage and in addition, they are joined to the autopalatine by ligaments. The antorbital is in
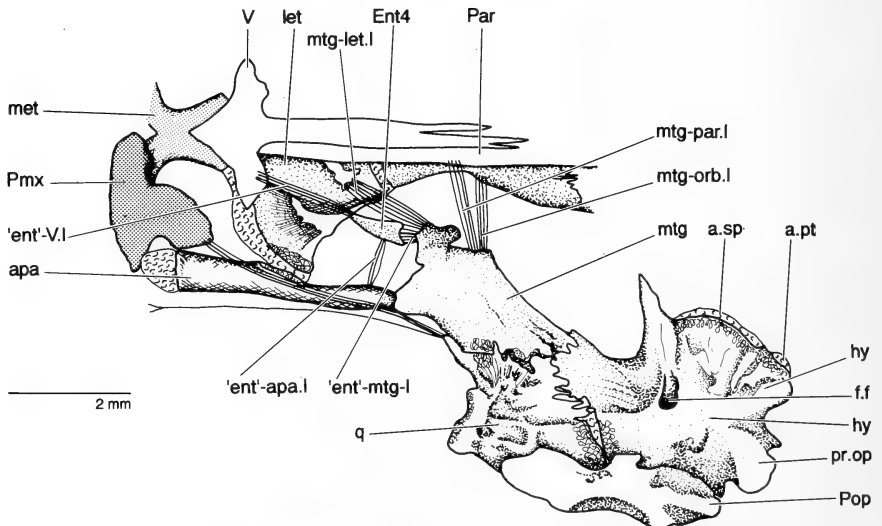
Fig.33: Suspensorium and its relationships in *Noturus exilis* (78 mm standard length; KU 172929) in ventral view of the premaxilla and anterior cranial bones.
apa: autopalatine; a. pt: articular facet for pterotic; a. sp: articular facet for sphenotic; Ent4: 'entopterygoid' type 4; 'ent'-apa. l: 'entopterygoid'-autopalatine ligament; 'ent'-mtg. l: 'entopterygoid'-metapterygoid ligament; 'ent'-V. l: 'entopterygoid'-vomer ligament; f.f: forament for hyoideomandibular nerve trunk; hy: hyomandibula; let: lateral ethmoid; met: mesethmoid; mtg: metapterygoid; mtg-let. l: metapterygoid-lateral ethmoid ligament; mtg-par. l: metapterygoid-parasphenoid ligament; mtg-orb.l: metapterygoid-orbitosphenoid ligament; Par: parasphenoid; Pmx: premaxilla; Pop: preopercle; pr. op: processus opercularis; q: quadrate; V: vomer.

close contact with this nodule of cartilage; it is attached to the posteromedial facet of the maxilla, the autopalatine, and the lateral ethmoid, as well as the nasal and/or premaxilla.

The complex quadrate is heavily ossified posteriorly, as well as in its articular region with the articular (lower jaw); whereas the anterodorsal part is thin and has numerous fine ridges. The complex quadrate articulates anteriorly through a short synchondral joint with the metapterygoid. The posteroventral region of the quadrate forms an articular facet for the preopercle.

The hyomandibula (Fig. 33) is a short, broad bone and its membranous outgrowth is comparatively smaller than that in *Trichomycterus areolatus* (Arratia 1990a). Dorsally the hyomandibula may have its elongate articular facet divided into three portions:
1) the dorsal portion of the anterior membranous outgrowth that articulates bone-to-bone in a groove of the sphenotic;
2) a long, cartilaginous surface for the sphenotic; and
3) a posterior, cartilaginous surface for the pterotic.

Only a few large specimens have three articular regions; portions two and three are usually combined. Posteriorly, the hyomandibula has a condylar articulation with the opercle, whereas it is sutured to the preopercle. Anteroventrally, the hyomandibula articulates synchondrally with the complex quadrate through the symplectic cartilage and anteriorly sutures (sutura dentata) with the quadrate and metapterygoid.

A long ligament extends branches from the quadrate to each of the following: the metapterygoid, autopalatine, premaxilla, and maxilla. The ligamentum primordiale is independent of this ligament as in *Trichomycterus areolatus* (Arratia 1990a). Several ligaments link the metapterygoid to surrounding bones: a broad ligament joins the metapterygoid to the orbitosphenoid, another ligament joins the metapterygoid to the lateral ethmoid, a third short ligament joins the metapterygoid to the 'entopterygoid' type 4. The 'entopterygoid' type 4 is linked through four separate ligaments to the metapterygoid, autopalatine, lateral ethmoid, and vomer. This 'entopterygoid' type 4 is consistently present.

The 'entopterygoid' type 4 of *Noturus* has fewer ligamentous connections (Fig. 2D) than the 'entopterygoid' in *Ameiurus melas* (Fig. 27A) and in *Ictalurus punctatus* (Figs. 2G, 27B). *Noturus* differs from *Ictalurus* and *Pylodictis* in the lack of a ligamentous connection between 'entopterygoid' and the orbitosphenoid.

'Pimelodids'

Heptapterus and *Parapimelodus* are currently included in the family Pimelodidae (e.g., Ringuelet et al. 1967, Eschmeyer 1990), in the subfamily Rhamdiinae (Lundberg et al. 1991); however, the 'Pimelodidae' are paraphyletic with respect to the Ariidae (see below).

Two patterns of the suspensorium are described below. First that of *Heptapterus mustelinus* is described, followed by that of *Parapimelodus valenciennesi*. The series of *Heptapterus mustelinus* examined included 12 cleared and stained specimens ranging in size from 27 mm to 185 mm standard length.
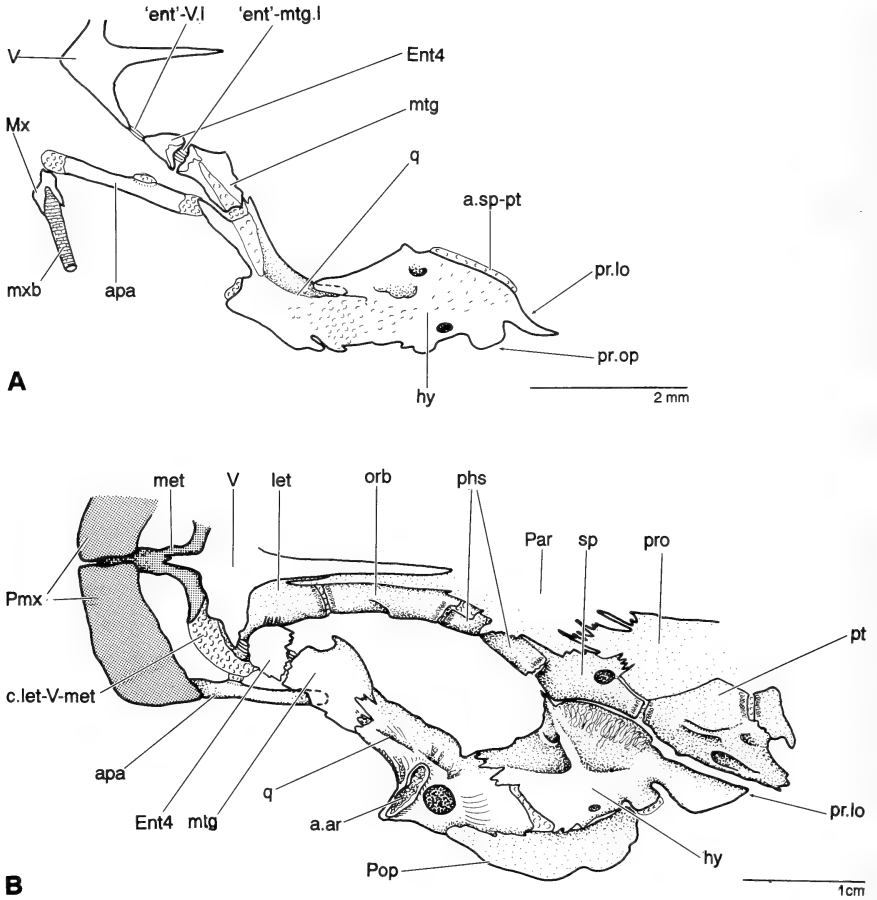
Fig.34: Suspensorium and its relationships in *Heptapterus mustelinus*. — A: Ventral view, 27 mm standard length (PC 50983); B: Ventral view, 185 mm standard length (PC 19484).
a.ar: articular facet for articular; apa: autopalatine; a.sp-pt: articular facet for sphenotic and pterotic; c.let-V-met: cartilage joining lateral ethmoid, vomer, and mesethmoid; Ent4: 'entopterygoid' type 4; 'ent'-mtg. l: 'entopterygoid'- metapterygoid ligament; 'ent'-V. l: 'entopterygoid'- vomer ligament; hy: homandibula; let: lateral ethmoid; met: mesethmoid; mtg: metapterygoid; Mx: maxilla; mxb: maxillary barbel; orb: orbitosphenoid; Par: parasphenoid; phs: pterosphenoid; Pmx: premaxilla; Pop: preopercle; pro: prootic; pr.lo: processus levator operculi; pr. op: processus opercularis; pt: pterotic; sp: sphenotic; q: quadrate; V: vomer.

In the 27 mm specimen of *Heptapterus*, every bone (Fig. 34A) of the palatoquadrate, hyoid, and branchial arches are already differentiated and partially ossified. The autopalatine is not connected by ligament or connective tissue to the metapterygoid during any stage of growth. The 'entopterygoid' type 4 is attached by a short ligament to the anterior part of the metapterygoid and by a little longer ligament to the lateral wing of the anterior part of the vomer. I could not find a ligament between the

'entopterygoid' and lateral ethmoid, except in large individuals. The 'entopterygoid' lies ventral to the lateral cartilage of the lateral ethmoid. Both an ectopterygoid and 'ectopterygoid' are absent. The metapterygoid (Fig. 34A) is slightly elongate; anteriorly it is heavily ossified and has a broad surface for the attachment of the 'entopterygoid'-metapterygoid ligament. The metapterygoid and hyomandibula are not sutured to each other during any stage of growth (Fig. 34A, B); both bones are completely separate due to the enlargement of the quadrate. A similar pattern is observed in other 'pimelodids' such as *Rhamdia, Pimelodus*, and *Parapimelodus*. The quadrate has an anterior, elongate, slightly-broad pterygoid process. The anterior membranous outgrowth of the hyomandibula is small in both young and adult individuals; the processus levator operculi is well developed.

The main ontogenetic changes of the bones of the suspensorium are related to size and position. For example, in large specimens the anterior part of the autopalatine rests largely on the dorsal face of the premaxilla. The medial articular facet of the autopalatine (Fig. 34B) articulates with the lateral ethmoid and with the ethmoidal cartilage joining the vomer, lateral ethmoid, and mesethmoid (as in diplomystids); a direct contact between the vomer and autopalatine is missing.

In large specimens the 'entopterygoid' (Fig. 34B) may articulate with the lateral ethmoid during growth, and a dentate and/or serrate sutural joint may form between the 'entopterygoid' and metapterygoid. Although the metapterygoid partly supports the eye, the eye is mainly resting on soft tissue between the suspensorium and neurocranium. A similar pattern is present in *Rhamdia*. The anterior membranous outgrowth of the hyomandibula is small and projects anteroventrally. Posterodorsally, the hyomandibula has a long, well-developed processus levator operculi (as it does in *Rhamdia*) that may extend nearly to the posterior end of the pterotic. The hyomandibula articulates mainly with the autosphenotic, and less extensively with the pterotic. The hyoideomandibular nerve trunk enters the hyomandibula medially and exits ventral to the opercular process.

The series of *Parapimelodus valenciennesi* examined included 12 cleared and stained specimens, ranging in size from 28—190 mm. In a 28 mm specimen, every bone of the palatoquadrate, hyoid and branchial arches has already differentiated and ossified; there are, however, slight changes in the shape of some bones during growth. The hyomandibula is dorsoventrally elongate and anteriorly has a moderate membranous outgrowth. The complex quadrate (Fig. 34A) has two well-defined parts: the posteroventral one articulates synchondrally with the hyomandibula and the anterior chondral process borders the membranous outgrowth of the hyomandibula and the metapterygoid. Anteriorly, the ectopterygoid process of the metapterygoid extends lateral to the autopalatine (Fig. 35A, B). The metapterygoid occupies the position that the ectopterygoid, entopterygoid, and metapterygoid occupy in other ostariophysans. The metapterygoid of *Parapimelodus* bears teeth on the medial surface of the broad, strong dorso-medial projection. From this observation it is evident that an early fusion between the chondral metapterygoid and a dermal toothplate has produced a compound dermo + metapterygoid bone (Fig. 35B, C).

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In some young and adult specimens, a small, elongate additional pterygoid type 1 (Fig. 35A) is present between the ventral part of the anterior membranous outgrowth of the hyomandibula and the dermo + metapterygoid; in other specimens, the pterygoid type 1 fuses to the dermo + metapterygoid. This additional pterygoid is apparently not a fracture of the dermo + metapterygoid.
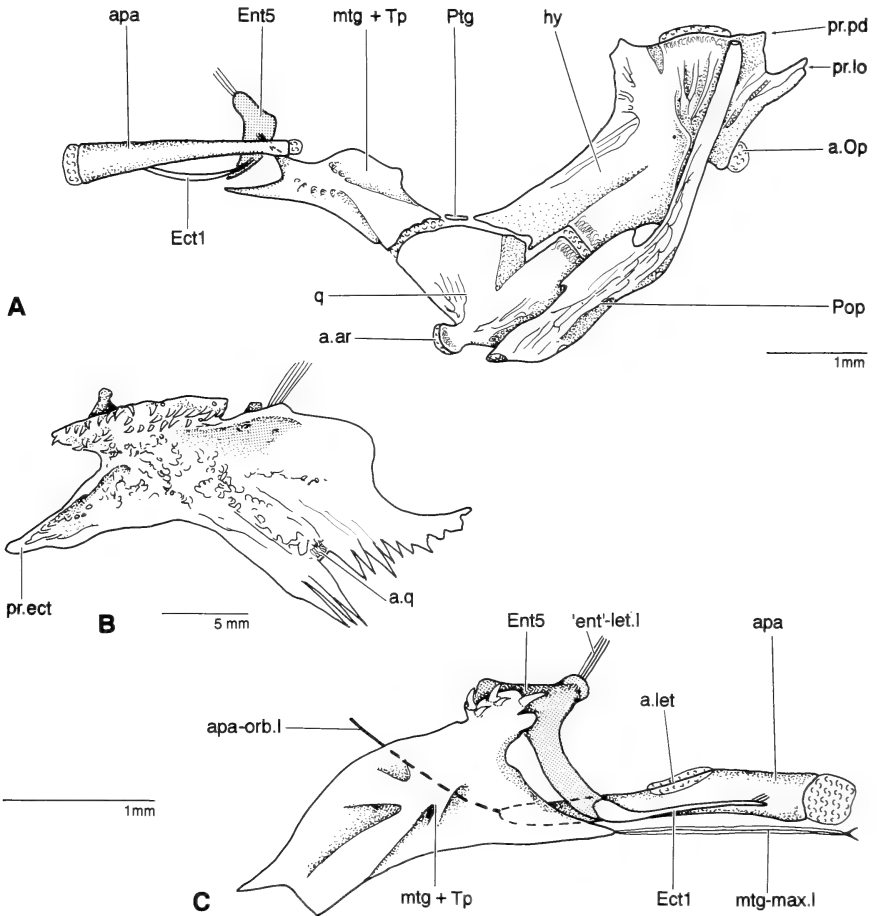
Fig.35: Suspensorium of *Parapimelodus valenciennesi*. — A: Suspensorium and preopercle, lateral view (41.6 mm standard length; ZMH 6669); B: Dermo + metapterygoid, medial view (190 mm standard length; KU 21084); C: Anterior part of the suspensorium, medial view (74.8 mm standard length; KU 21084).
a.ar: articular facet for articular; a.let: articulation for lateral ethmoid; a.Op: articular facet for opercle; apa: autopalatine; apa-orb.l: autopalatine-orbitosphenoid ligament; a.q: articular facet for quadrate; Ect1: 'ectopterygoid' type 1; Ent5: 'entopterygoid' type 5; 'ent'-let.l: 'entopterygoid'- lateral ethmoid ligament; hy: hyomandibula; mtg+Tp: dermo + metapterygoid; mtg-max.l: metapterygoid-maxillary ligament; Pop: preopercle; pr.ect: processus ectopterygoideus; pr.pd: processus posterodorsalis; pr.lo: processus levator operculi; Ptg: pterygoid type 1; q: quadrate.
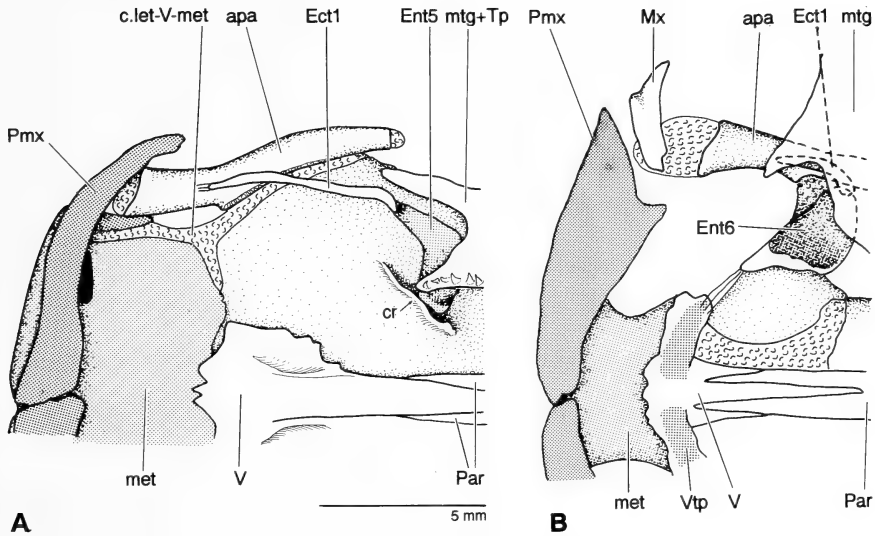
Fig.36: Autopalatine and surrounding bones, ventral view. — A: *Parapimelodus valenciennesi* (175 mm standard length; KU 21804); B: *Bagre marinus* (78.6 mm standard length; KU 3053). A,B same scale.
apa: autopalatine; c.let-V-met: cartilage joining lateral ethmoid, vomer, and mesethmoid; cr: crest; Ect1: 'ectopterygoid' type 1; Ent5-6: 'entopterygoid' types 5-6; met: mesethmoid; mtg: metapterygoid; mtg+Tp: dermo+metapterygoid; Mx: maxilla; Par: parasphenoid; Pmx: premaxilla; V: vomer; Vtp: vomerine toothplate.

In both small and large specimens, an elongate 'ectopterygoid' type 1 (Figs. 35A—C, 36A) lies ventral to the autopalatine. It is sharp anteriorly and curves posteromedially. Its posterior end is ligamentously attached to 'entopterygoid' type 5.

Anteriorly, the elongate autopalatine has a large nodule of fibrocartilage in adults. The small articular facets of the maxilla articulate with this fibrocartilage, which also abuts a cavity in the dorsal aspect of the premaxilla. Medially, the autopalatine articulates via cartilage with the lateral ethmoid. This cartilage reaches the mesethmoid but not the vomer in large individuals (Fig. 36A).

The 'ectopterygoid' type 1 is joined anteriorly by a short ligament to the autopalatine, and posteriorly to the 'entopterygoid' type 5. The 'entopterygoid' type 5 is also connected by short ligaments to the 'ectopterygoid' type 1, the dermo+metapterygoid, and lateral ethmoid. There is no ligament between the autopalatine and dermo+metapterygoid. A strong ligament extends from the ectopterygoid process of the metapterygoid to the maxilla, but a ligamentous link between metapterygoid and vomer is absent. A ligament extends from the posterior part of the autopalatine to the posterior part of the orbitosphenoid. There is no link between the metapterygoid-maxillary ligament and the ligamentum primordiale that extends from the coronoid cartilage of the lower jaw to the premaxilla. The autopalatine is attached by ligaments to the lateral ethmoid and antorbital. The antorbital is also attached to the premaxilla and nasal.

Regan (1911: 572) arranged some of the genera of pimelodids into subfamilies, accor-

ding to the presence or absence of the 'ectopterygoid' type 1 and features of the 'entopterygoid' type 5 (shape and attachment and/or articulation with the lateral ethmoid and metapterygoid). Gosline (1975) considered the two dermal ossifications as (fractures of the) entopterygoid, but my observations of the early ontogeny of 'pimelodids' do not support such an hypothesis. *Parapimelodus* has the same 'ectopterygoid' type 1 as described in *Callophysus, Pimelodus, Piramutana*, and *Sciades* (Regan 1911), but it has teeth on the dermo + metapterygoid which are not described for other pimelodids.

Recently, Lundberg et al. (1991) characterized the subfamily Rhamdiinae by five synapomorphies, two of which are characters of the suspensorium. These are the process for insertion of the levator operculi muscle greatly expanded and adjacent to the pterotic, and quadrate with a free dorsal margin and a bifid shape. Both features are homoplastic; they are found in certain other 'pimelodids' and in other catfishes like certain 'bagrids'.

'Bagrids'

My interpretation of the pterygoid series is somewhat different from those of Tilak (1965), Jayaram (1966), and Mo (1991). According to Tilak (1965), the entopterygoid is absent in *Mystus, Rita*, and *Horabagrus*; however, the small, bent and rod-shaped bone that he identified as the ectopterygoid is joined by a ligament to the metapterygoid (Tilak 1965: Figs. 14, 15, 17), a role of the 'entopterygoid' in other catfishes.

The complex metapterygoid in 'bagrids' may or may not contact the hyomandibula. A small metapterygoid that has no contact with the hyomandibula is present in *Mystus (Mystus)* (Tilak 1965: Figs. 15, 16) and *Rita rita* (Mo 1991: Fig. 47); this is a specialization of these 'bagrids' compared to other catfishes (Joseph 1960). This condition, however, is also present in the 'pimelodids' *Heptapterus, Rhamdia*, and *Parapimelodus*. A sutural contact is found in 'bagrids' such as *Horabagrus* and *Mystus (Osteobagrus)* (Tilak 1965: Figs. 14, 17).

Schilbeids

My interpretation of the pterygoid series is somewhat different from those of Tilak (1961) and Gosline (1975) for *Eutropiichthys vacha*. A large bone synchondrally and suturally articulates with the quadrate. Based on its ontogenetic origin, this bone must be the metapterygoid (Fig. 37A), which dorsally occupies the position of the entopterygoid in other teleosts (excluding siluroids). A long, dentate bone identified as the ectopterygoid by Tilak (1961) and as a tooth plate by Gosline (1975) lies ventrolateral to the complex quadrate and metapterygoid. This bone broadens anteriorly and broadly extends below the small autopalatine. It partially occupies the position of ectopterygoid and dermopalatine in primitive teleosts, and therefore could be interpreted as ectopterygoid + dermopalatine (Fig. 37A, B). However, another interpretation could be that this bone is just a long dentate ectopterygoid; a third interpretation could be that this bone is a new formation. This third interpretation is the most reasonable approach if we study the distribution of this feature among siluriforms. Based on its position and comparison with other siluriforms, I identify it as a lateral toothplate; another additional element of the suspensorium of catfishes.
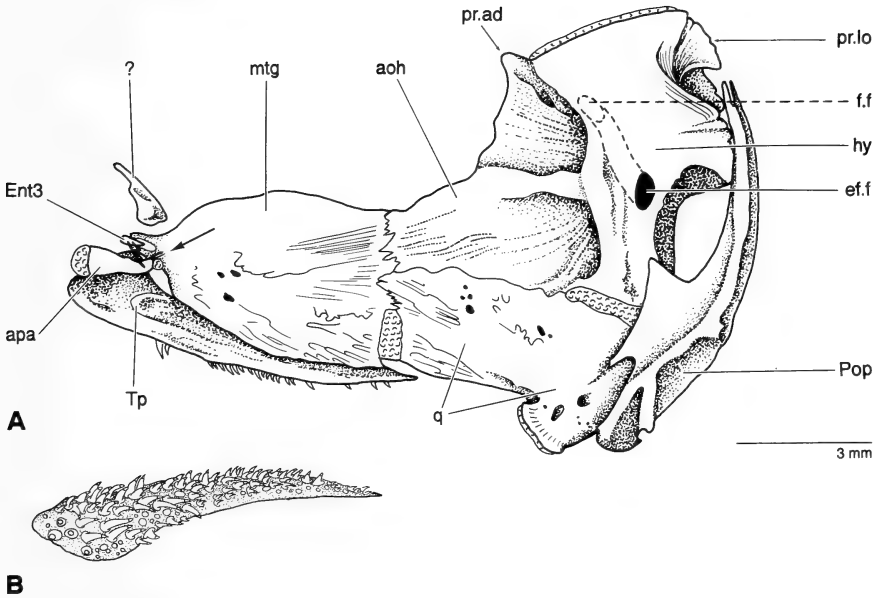
Fig.37: Suspensorium and preopercle of *Eutropiichthys vacha* (109 mm standard length; KU 12169). — A: Lateral view; arrow points to the autopalatine-metapterygoid ligament; B: Lateral toothplate, ventral view. Scale applies to both figures.

aoh: membranous outgrowth; apa: autopalatine; ef.f: exit foramen of the facial nerve; Ent3: 'entopterygoid' type 3; f.f: foramen for the passage of facial nerve; hy: hyomandibula; mtg: metapterygoid; Pop: preopercle; pr.ad: processus anterodorsalis; pr.lo: proccesus levator operculi; q: quadrate; Tp: lateral toothplate; ?: additional pterygoid?

The autopalatine is a small rod-like bone, that has cartilage both anteriorly and posteriorly. The small maxilla articulates through two small facets with the anterior autopalatinal cartilage. The anterior cartilage also rests on the posterior margin of the premaxilla. In *Ailia coilia* the autopalatine articulates with both the maxilla and the antorbital. In *Eutropiichthys*, the antorbital articulates with the lateral ethmoid (but not the maxilla) and is attached by ligaments to the autopalatine, premaxilla, and to the base of the nasal barbel.

Anteriorly, the metapterygoid produces two small projections. An 'entopterygoid' type 3 is located between the projections. The large metapterygoid is laterally sutured to the lateral tooth plate, and posterodorsally sutured to the hyomandibula and quadrate. In addition, a synchondral articulation is present between the lateral part of the metapterygoid and the pterygoid process of the quadrate.

In the specimen studied here, there is an additional small, flat bone present. It is medial to the metapterygoid and was not mentioned by Tilak (1961), and its presence is probably variable. This bone is free; I could detect no ligamentous, or other connection joining it to any surrounding bones.

The quadrate is a large bone, almost rectangular; with an elongate chondral pterygoid process that dorsally bears a membranous outgrowth. This membranous outgrowth is

sutured to the metapterygoid and hyomandibula. In addition, the quadrate articulates with the hyomandibula through the symplectic cartilage. Posteriorly, the quadrate shares a suture with the preopercle. The preopercle also shares a short suture with the hyomandibula.

Short ligaments extend between the 'entopterygoid' type 3 and the metapterygoid, autopalatine, and lateral ethmoid. In addition, strong ligaments extend from the medial face of the metapterygoid to the lateral ethmoid and orbitosphenoid. I was unable to find a ligamentous connection between the autopalatine and orbitosphenoid; therefore, the most posterior ligament of the autopalatine is the autopalatine-metapterygoid ligament.

Tilak (1961) described a metapterygoid, a toothed ectopterygoid, and a small entopterygoid in *Eutropiichthys vacha*. Gosline (1975: 7) stated that in catfishes there is often a tooth-bearing plate on the oral surface of the metapterygoid-vomer ligament and that such a plate has frequently been identified as an ectopterygoid. Such an identification is questionable. "Sometimes part or all of such tooth plate becomes firmly attached to the metapterygoid as in the schilbeid *Eutropiichthys* (Tilak 1961: Figs. 7, 8)" (Gosline 1975: 7). I disagree with this interpretation of Tilak's figures because the specimen studied here (KU 12169) does not have a metapterygoid-vomer ligament. Instead it has a metapterygoid-lateral ethmoid ligament. Furthermore, this metapterygoid cannot be readily compared to the so-called ectopterygoid of Tilak (1961), or to that described by other authors. The bone identified as the entopterygoid by Tilak (1961) is considered here (by comparison with other ostariophysans) to be an 'entopterygoid' type 3.

Trichomycterids

A detailed description of the suspensorium of trichomycterids and of related literature is found in Arratia (1990a).

COMPARISON AMONG CERTAIN SILURIFORMS

The origin of the metapterygoid from the hyo-symplectic-pterygoquadrate plate takes place in two unique ways. This separates the siluroids into two groups:

(1) Siluroids with a small pars quadrata, where the metapterygoid arises as a perichondral ossification of an anterior cartilaginous projection — the pterygoid process — dorsal to the quadrate region of the hyo-symplectic-pterygoquadrate plate. Examples include diplomystids (Fig. 16A, B; Arratia 1987a: Fig. 25B), *Ictalurus* and *Pylodictis* (Figs. 24C, 25A), nematogenyids (Fig. 28A; Arratia 1990a: Fig. 12A, B), loricariids (Arratia 1990a: Fig. 13A—C), and callichthyids (Arratia 1990a).

(2) Siluroids with a complex quadrate, where the metapterygoid arises as a perichondral ossification of the anterior projection — the pterygoid process — of the large pars quadrata, and articulates both synchondrally and suturally with the anterior part of the chondral and membranous projection of the quadrate. Examples include *Heptapterus* (Fig. 34A), *Parapimelodus* (Fig. 35A), and Trichomycteridae (Arratia 1990a: Figs. 3A—D, 5A, B).

The first pattern is exhibited by the primitive diplomystids and within the loricarioids, by the nematogenyids and advanced loricariids. The second pattern is also exhibited by primitive and advanced siluroids. Both patterns may even be found in a single family; for example, both *Ictalurus* and *Pylodictis* have a simple quadrate, whereas *Noturus* has a complex quadrate (which represents the advanced condition among the Ictaluridae). The quadrate exhibits several evolutionary transformations among loricarioids. For example, *Nematogenys* has a short, broad quadrate similar to that of diplomystids and representative of the primitive condition. Loricariids have a simple, deep, narrow quadrate. Among loricarioids, a complex quadrate is found in the Trichomycteridae and Astroblepidae; however, the ontogenetic origin of the pterygoid process differs between them (Arratia 1990a).

Autopalatine

The length of the autopalatine in siluroids differs from group to group. The autopalatine is long early in ontogeny and stays long throughout growth, retaining large cartilaginous regions anteriorly and posteriorly, in *Diplomystes camposensis* within the Diplomystidae (Fig. 17A, B). In contrast, it is short in *Diplomystes chilensis* (Fig. 17C). The autopalatine is very small in *Eutropiichthys* (Fig. 37A) and *Ailia*; and it has atrophied to articulate posteriorly with the maxilla and lateral ethmoid in *Euchilichthys guentheri* (Starks 1926: Fig. 15); it is a small hoof-shaped nodular element in Siluridae (Howes & Ayanomiya Fumihito 1991: Fig. 13).

A rod-shaped autopalatine (Fig. 26A, B) seems to be most common in siluroids. However, young diplomystids and juvenile diplomystids have an anteriorly broad autopalatine (Figs. 16A—C, 17A, B) that is forked into two long maxillary processes. This is unique to the Diplomystidae. Grande (1987) noted that Tilak (1964) figured the autopalatine of *Ailia coila* with an anterior fork; however, it is not forked in the cleared and stained specimen KU 12156. Grande (1987) refers to a distinct notch in the anterior part of the autopalatine of Diplomystoidei based on Fink & Fink (1981: Fig. 11) and his examination of a single specimen of *Olivaichthys viedmensis*. Specimen MCZ 8290 figured in Fink & Fink (1981: Fig. 11) and in Arratia (1987a: Fig. 6A) does not have a notch. In both *Diplomystes chilensis* and *Olivaichthys viedmensis* both of the anterior elongate processes of the autopalatine fuse during ontogeny to leave only a foramen (Fig. 17C); whereas in *Diplomystes nahuelbutaensis* and *D. camposensis* both processes stay separate (as in early ontogeny) and therefore a deep notch is observed (Arratia 1987a: Figs. 14B, 24B, 25A—D). The autopalatine is broader anteriorly than posteriorly in †*Hypsidoris* and *Nematogenys*, but *Nematogenys* lacks the two maxillary processes. It is unknown if †*Hypsidoris* has two anterior maxillary processes in early ontogeny. The autopalatine is more or less triangular in *Trichomycterus*, although it may have an enormous anterior extent in some trichomycterids (Arratia 1990a: Fig. 11A).

In most catfishes, the antorbital is ligamentously attached to the autopalatine anteriorly (Fig. 38A—G), whereas these bones articulate in *Ailia*. The autopalatine does not articulate nor is it connected to infraorbital bones in some siluroids (including *Hypostomus* and *Callichthys* [Arratia 1987a, 1990a]).

The autopalatine is linked to the premaxilla in as many as six different ways:

(1) directly through the anterior nodule of cartilage of the autopalatine that laterally abuts against a cavity or the dorsal surface of the premaxilla (e.g., Siluroidea sensu Grande 1987);

(2) directly through a small ligament or short length of connective tissue that extends between the medial side of the anterior nodule of cartilage of the autopalatine and the premaxilla (e.g., *Olivaichthys* and *Nematogenys*);

(3) directly through the anterior nodule of cartilage that during ontogeny medially produces an articulation with the premaxilla (e.g., *Trichomycterus, Bullockia*, and *Eremophilus*);

(4) an indirect link through the antorbital, that is joined by ligaments to the autopalatine and premaxilla (e.g., *Parapimelodus, Eutropiichthys*, and a few specimens of *Noturus*);

(5) an indirect link through the maxilla, that articulates with the autopalatine and is joined to the premaxilla by a ligament (e.g., *Trichomycterus*);

(6) no link at all (e.g., *Diplomystes camposensis*).

The autopalatine articulates medially with cranial bones such as the lateral ethmoid and vomer in primitive catfishes. Diplomystids seem to be unique in that the articular facet with the vomer is also connected by a small amount of cartilage to the mesethmoid, lateral ethmoid, and orbitosphenoid. A similar joint is found in *Nematogenys, Rhamdia*, and *Heptapterus*, but a connection with the orbitosphenoid is missing. A direct articulation between autopalatine, lateral ethmoid, and vomer is present in trichomycterines. In adult *Parapimelodus* and ictalurids there is no direct or indirect articulation between autopalatine and vomer.

Burne (1909) found that the autopalatine impinged on the wall of the nasal cavity in *Clarias* and *Malapterurus*; he suggested that movements of the autopalatine would alter the volume of the nasal cavity as well as the movement of the barbels (nasal and maxillary). The autopalatine partially frames the wall of the nasal cavity in most catfishes including the diplomystids (Arratia 1987a) and it is attached to the antorbital (which also frames the nasal cavity). The antorbital may also be connected to the posterior nostril (Fig. 38A, B), or to the nasal bone (Fig. 38C—E), or to the base of the nasal barbel (Fig. 38F), or to the cartilaginous support of the nasal barbel (Fig. 38G). The antorbital has a dorsal projection that extends between both nostrils and is attached to the nasal bone in *Arius*.

The relationships of the anterior part of the autopalatine have to be extensively studied in many other catfishes. Only in this way will we learn about the distribution and evolutionary relationships among the seven patterns of articulation and linkage (Fig. 38A—G) presented here (other patterns may also be added by studying other catfishes).

The posterior part of the autopalatine may occupy the following positions in adult specimens of different catfish groups:

1. The posterior cartilage of the autopalatine borders 'entopterygoid' type 2 and the metapterygoid. These three bones are in the same plane (unlike other catfishes) and the short ectopterygoid process of the metapterygoid is lateral to the autopalatine.
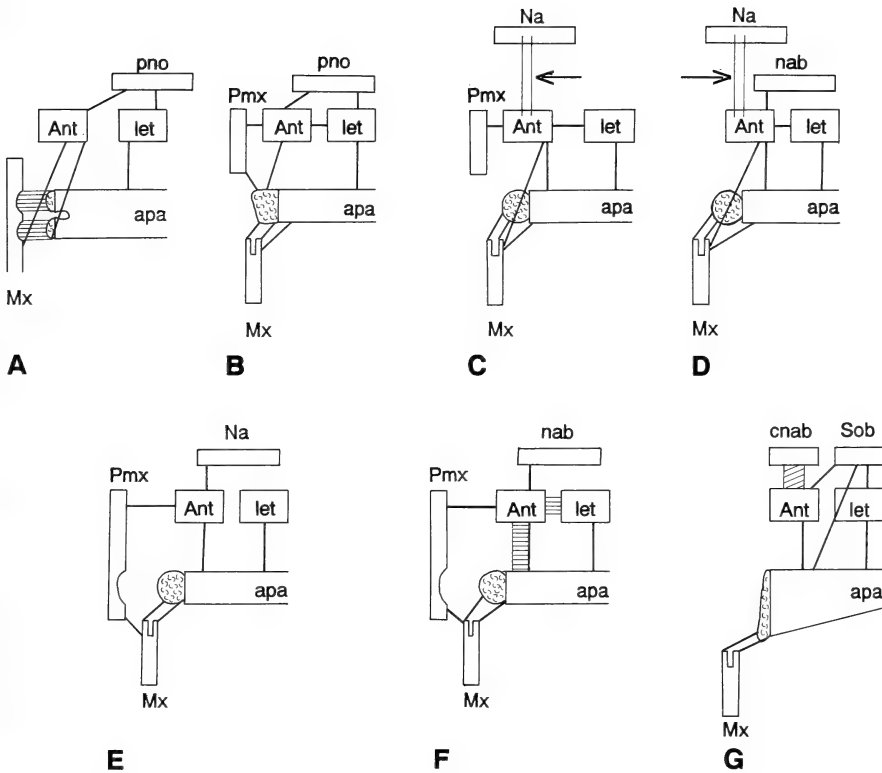
Fig.38: Attachments of the anterior part of the autopalatine to the surrounding bones, posterior nostril, and base of the nasal barbel in certain siluriforms. Arrow points to the intersection of the infraorbital and supraorbital sensory canals. A bar with horizontal lines represents an articulation. A bar with oblique lines represents a close attachment between the antorbital and cartilaginous support plate of the nasal barbel. — A: *Diplomystes* and *Olivaichthys*; B: *Nematogenys*; C,D: *Noturus*; E: *Parapimelodus*; F: *Ailia*; G: *Trichomycterus*.
Ant: antorbital; apa: autopalatine; cnab: cartilaginous plate supporting the nasal barbel; let: lateral ethmoid; Mx: maxilla; Na: nasal bone; nab: nasal barbel; Pmx: premaxilla; pno: posterior nostril; Sob: 'supraorbital'.

This state is known only in Nematogenyidae (Fig. 28B; Arratia 1990a).

2. The posterior cartilage of the autopalatine borders the entopterygoid (when present) and is dorsal to 'entopterygoid' type 1 (when present). The long ectopterygoid process of the metapterygoid is lateral to the autopalatine. This state is only known in Diplomystidae (Figs. 16A, C, 19A—D).

3. The posterior part of the autopalatine is dorsal to the metapterygoid and is not in contact with any dermal pterygoid. This state is observed in many catfishes, e.g., trichomycterines (Arratia 1990a: Figs. 7, 8), *Noturus* (Figs. 32C, 33), *Parapimelodus* (Figs. 35A, 36A), and *Eutropiichthys* (Fig. 37A).

4. The posterior part of the autopalatine extends dorsal or dorsolateral to the 'entopterygoid', not the metapterygoid. This pattern is found in ictalurids such as *Ameiurus melas, Ictalurus furcatus, I. punctatus,* and *Pylodictis* (Fig. 27A—D).

5. The posterior part of the autopalatine articulates with the lateral ethmoid and is dorsal to the metapterygoid. This pattern is found in *Loricaria, Loricarichthys* (Arratia 1990a: Fig. 13A, B), and *Callichthys*.

The posterior end of the autopalatine in catfishes may or may not have a large nodule of cartilage, or fibrocartilage in adults. A posterior cartilage is present in siluriforms such as the Diplomystidae, Ictaluridae, *Parapimelodus*, and *Eutropiichthys*; this cartilage is absent in the Trichomycteridae and Loricariidae (Arratia 1990a). Although the posterior cartilage is present in a variety of catfishes, only it forms an articular surface for the entopterygoid in the Diplomystidae and for 'entopterygoid' type 2 in the Nematogenyidae. In other siluroids, the posterior cartilage does not articulate with the sesamoid 'entopterygoids'.

The posterior part of the autopalatine may or may not be connected to the orbitosphenoid or pterosphenoid by a ligament (e.g., to the orbitosphenoid in Diplomystidae and *Parapimelodus*; to the pterosphenoid in *Trichomycterus*). The lack of a direct ligamentous link between the autopalatine and orbitosphenoid or pterosphenoid is characteristic of siluroids such as *Ictalurus, Pylodictis, Noturus, Eutropiichthys*, and *Nematogenys*. However, an indirect link between the autopalatine and orbitosphenoid is achieved through a 'entopterygoid' in *Ameiurus, Ictalurus*, and *Pylodictis*.

The autopalatine is directly connected to the metapterygoid by one (ligament 17 of Ghiot 1978, Ghiot et al. 1984) or two ligaments or connective tissue (e.g., diplomystids, nematogenyids, and ictalurids) or indirectly by ligamentous connections through a sesamoid 'entopterygoid' (e.g., *Bagre, Galeichthys*, and *Parapimelodus*).

Subautopalatine toothplate

Ostariophysans do not have a dermopalatine (Fink & Fink 1981: 315); however, dentate elements associated with the autopalatine are present in some catfishes; recently, Howes & Ayanomiya Fumihito (1991) considered that the posterior extension of the autopalatine of siluroids is probably the dermopalatine. The development of the catfishes studied herein does not support such a hypothesis. Large individuals of the diplomystid *Olivaichthys* have a tooth patch attached by a ligament to the autopalatine; this element was identified as the dermopalatine by Arratia (1987a), who considered the presence of a dermopalatine appearing late in ontogeny to be an autapomorphy of *Olivaichthys*. In contrast, in *Amia* and primitive teleosts, the dermopalatine ossifies before the autopalatine (Arratia & Schultze 1991: Table 1).

Starks (1926: Fig. 12) figured a large 'dermopalatine' closely associated with the medial face of the vomerine toothplate and posterior to a parasphenoid toothplate in an adult 'pimelodid', *Sciadeichthys troscheli*. Recently Bailey & Stewart (1984: Figs. 2B, 5a—c) labelled a bagrid toothplate as the dermopalatine; this element is partially ventral to the autopalatine. Skelton et al. (1984) named a similar toothplate in 'bagrids' as the subpalatine. Grande (1987) however, named two plates present in †*Hypsidoris* as accessory ectopterygoid toothplates. One toothplate is ventral to the autopalatine (as in *Olivaichthys*) and the other toothplate is between the vomerine toothplate and the autopalatine (Fig. 22C). Unfortunately, this position has no connection with any ec-
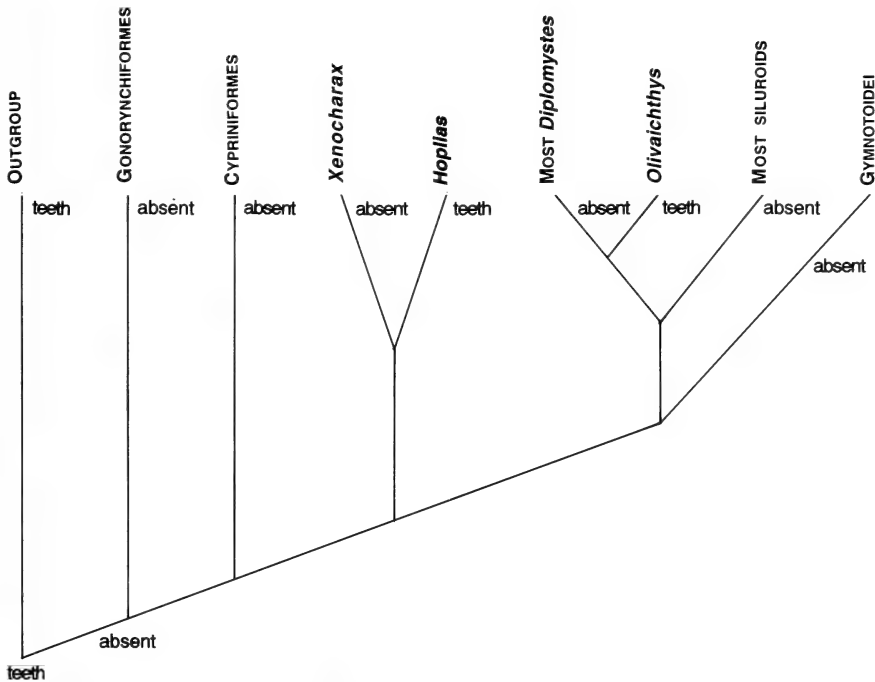
Fig.39: Distribution of autopalatal toothplate in ostariophysans (hypothesis of relationships after Fink & Fink 1981). — absent: absence of toothplate; teeth: toothplate attached or fused to autopalatine.

topterygoid (even if this were present) and therefore the name accessory ectopterygoid toothplate is inappropriate in the absence of any convincing evidential support. While information on the ontogeny of the suspensorium is unavailable for some groups, it is not possible to judge whether the toothplate originates ventral to the autopalatine, or whether it is a displaced vomerine toothplate. I will therefore consider the dentate plate ventral to the autopalatine as a subautopalatine toothplate.

The distribution of the character — absence of dermopalatine (Fig. 39) — in ostario-physans, leads to the conclusion that the subautopalatine toothplate present in *Hoplias*, in some diplomystids, †hypsidorids, 'pimelodids', and 'bagrids' is a new formation. Because ontogenetic studies of most siluroids are lacking, as are detailed studies of larger individuals, it is uncertain how widespread the presence of the subautapalatine toothplate is among 'pimelodids', ariids, and 'bagrids'. A subautopalatine toothplate has not been observed in large ictalurids.

Antorbital

Although the antorbital is not part of the suspensorium, I will discuss here its connection with the suspensorium. The antorbital — highly modified in shape and size (Ar-ratia 1987a) — connects by ligaments to the autopalatine, maxilla, and lateral ethmoid in most of the catfishes studied here (Fig. 38A—G). It may also be connected with the

premaxilla (e.g., *Nematogenys, Ailia, Parapimelodus*, and some specimens of *Noturus*). The antorbital is connected with the 'supraorbital' (united by a ligament with the frontal) in *Trichomycterus* (Fig. 38G) as well as in other trichomycterids. There is no doubt that the antorbital has a sensory function because it carries the anterior part of the infraorbital sensory canal. In addition, it also participates in the movement of the maxillary barbel through its ligamentous connections to the autopalatine, maxilla, lateral ethmoid, and other bones (Fig. 38A—G). These facts characterize the siluroid antorbital (a synapomorphy of siluroids?). (A dermal antorbital that is attached by connective tissue to the lateral ethmoid, autopalatine, and maxilla is found in primitive characiforms.) The articulation of the antorbital with the autopalatine (Fig. 38F) present in some siluroids, is considered here to be an advanced condition present only in a few groups such as the schilbeids.

Metapterygoid

According to my studies, the only pterygoid bone consistently present in siluroids is the metapterygoid. Although it is a chondral bone, its appearance varies within catfishes. It is mainly formed as a perichondral ossification of pars metapterygoidea in diplomystids. The perichondral ossification is restricted to a small area in *Parapimelodus, Noturus, Eutropiichthys*, and all other siluroids studied here. Enlargement of the bone is achieved mainly by membranous outgrowths.

The metapterygoid in catfishes commonly occupies the position of both the ectopterygoid and entopterygoid in other teleosts. According to Boulenger (1904) and Hashmi (1957) the metapterygoid is absent in Siluridae. Starks (1926) identified the bone anterior to the quadrate as the ectopterygoid. Starks (1926: 324—325) based his identification on the fact that he "knows of no case where the pterygoid (ectopterygoid) if present is separated from the quadrate", "the metapterygoid, if represented at all, may be incorporated with the pterygoid; but it may be as well incorporated with the hyomandibular". The last interpretation has also been followed by Hoedeman (1960), Arratia & Menu Marque (1981, 1984), Arratia et al. (1978), Howes (1985), and Howes & Teugels (1989). However, Arratia (1990a) showed that the hyomandibula and metapterygoid are independent bones in loricarioids. Recently, Howes & Teugels (1989) interpreted the metapterygoid of some siluroids as a compound bone which in addition to the metapterygoid itself may include the ectopterygoid and entopterygoid. Since these authors did not offer evidence supporting such an interpretation and my observation on ontogenetic series does not support them, I will not discuss Howes & Teugels interpretation further.

In catfishes the metapterygoid (Lundberg 1982, Howes 1985, Arratia 1987a) commonly overlaps the anterior membranous outgrowth of the hyomandibula, similar to the position of the palatoquadrate cartilage in early ontogeny of other teleosts. Exceptions where the bones do not overlap, include siluroids such as the 'pimelodids' *Heptapterus, Rhamdia*, and *Parapimelodus* (Figs. 34A, B, 35A), and the 'bagrids' *Pseudeutropius atherinoides* (Tilak 1964: Fig. 20) and *Bagrus bayard* (Skelton et al. 1984: Fig. 15A). A very narrow overlap is present in *Nematogenys* (Fig. 28D).
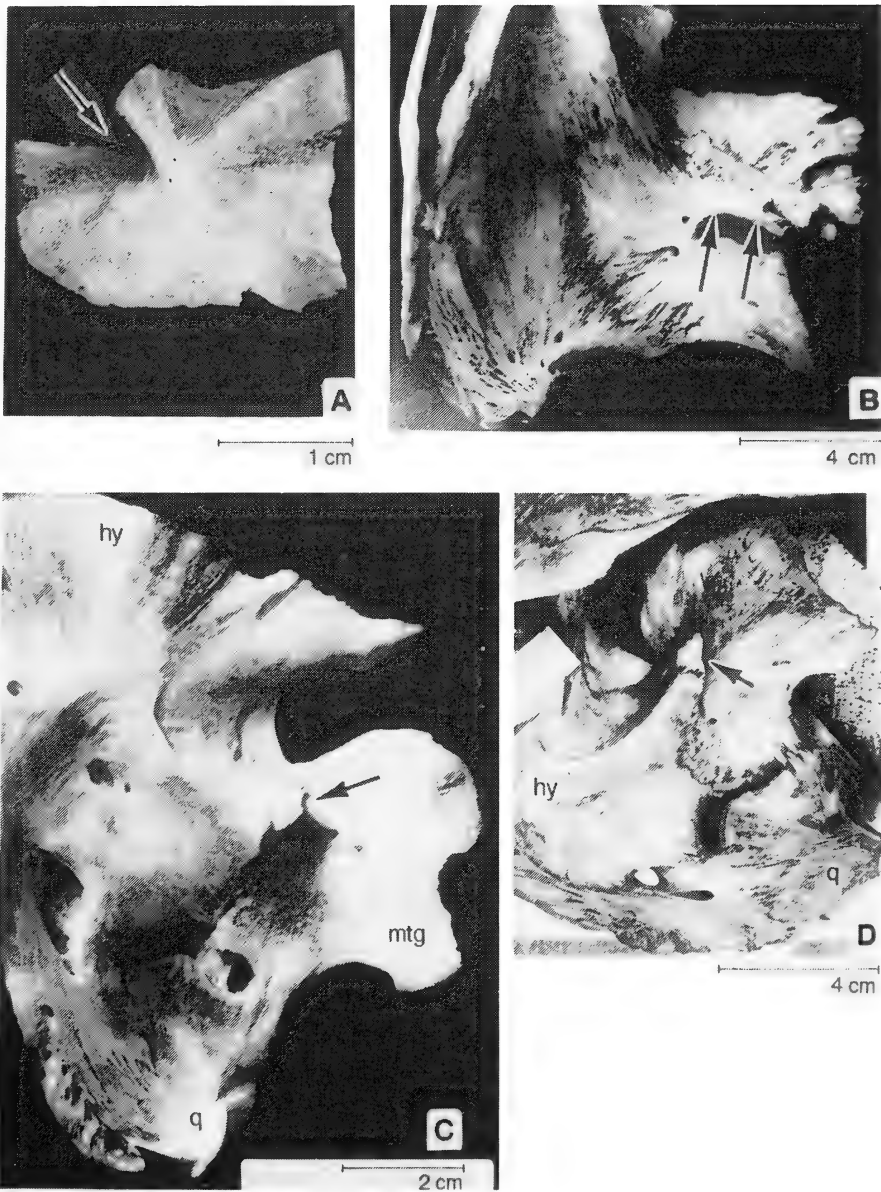
Fig.40: Metapterygoid, lateral views. — A: *Amia calva* (disarticulated specimen; KU uncat.); arrow points to a notch; B: *Pylodictis olivaris* (neurocranium of 360 mm in length; KU 13122); C: *Ictalurus furcatus* (neurocranium of about 270 mm in length; KU 15866); D: *Ictalurus furcatus* (neurocranium of about 280 mm in length; KU 11343). B—D, Arrows point to the 'lateral process' of metapterygoid.
hy: hyomandibula; q: quadrate.

An enormous metapterygoid (which forms much of the palatal region) is characteristic of *Eutropiichthys* (Fig. 37A), whereas a rudimentary metapterygoid is present in advanced trichomycterids such as tridentines and vandellines (Arratia 1990a: Figs. 11A—C). In the trichomycterid *Ochmacanthus* the autopalatine enlarges to form most of the palate. These are examples of the widely divergent patterns of construction of the palatal region in catfishes.

The metapterygoid in catfishes such as diplomystids (Figs. 17A, 18C), †*Hypsidoris* (Fig. 22D), and *Parapimelodus* (Fig. 35A), has a dorsal notch separating the processus basalis and the posterodorsal part of the metapterygoid as in *Amia* and primitive teleosts (Fig. 40A; Arratia & Schultze 1991: Figs. 1D, 15B, 20A, 23, 24). The processus basalis is small or absent in advanced siluroids (e.g., *Trichomycterus, Eutropiichthys*).

A well-developed 'lateral process' is consistently present on the lateral surface of the metapterygoid in ictalurids such as *Pylodictis olivaris* (Fig. 40B; Lundberg 1982: Fig. 25C) and in large *Ictalurus furcatus* (Fig. 40C—D). Based on the distribution of this character among ostariophysans, the 'lateral process' present in *Pylodictis* is non-homologous with the processus metapterygoideus lateralis present in *Amia* and primitive teleosts (Arratia & Schultze 1991: Figs. 20A, 23, 24), because it is missing in more primitive catfishes as well as in other primitive ostariophysans. Instead it is a specialization of primitive ictalurids in which the process serves as attachment for the anteriormost section of the levator arcus palatini muscle.

The ventrolateral or anterolateral projection of the metapterygoid is named here the ectopterygoid process because it occupies the position of the ectopterygoid in other teleosts. There is no ontogenetic evidence that would cause us to consider the process as a fused ectopterygoid, as proposed by Howes & Teugels (1989). The ectopterygoid process is variable in extent in primitive catfishes and may be a well-developed sharp projection (Figs. 17A—C, 18C, 35A, B), or a moderately long, slightly expanded projection (Figs. 28B, 32) or a rudimentary projection (Fig. 26C). Large *Ictalurus furcatus* may not have the process at all. Advanced catfishes such as the trichomycterids lack the basal, lateral metapterygoid, and ectopterygoid processes; this combination of features is an advanced one within catfishes.

The joint between the posteroventral part of the metapterygoid and the anterior or anterodorsal part of the quadrate is a unique feature of siluroids within the teleosts. In other teleosts, the ventral or anteroventral part of the metapterygoid articulates with the posterior, posterodorsal or anterodorsal part of the quadrate. Within siluroids, the joint between the ventral part of the metapterygoid and anterodorsal part of the quadrate is interpreted as the primitive condition, retained in diplomystids and nematogenyids. The joint between the posteroventral part of the metapterygoid and anterior projection of the quadrate is shared by several siluroids including ictalurids, trichomycterids, pimelodids, and schilbeids. The joint between the metapterygoid and symplectic cartilage in diplomystids and nematogenyids is interpreted as a derived feature within siluroids. This state is not homologous to the situation found in the clupeomorph *Denticeps* (Arratia & Schultze 1991: Figs. 28A, B), cypriniforms (Fig. 8A, B) or

characiforms (Fig. 10A), because the development of the metapterygoid differs between siluroids and other ostariophysans.

The posterodorsal part of the metapterygoid is commonly sutured (sutura serrata or dentata) with the anteroventral part of the anterior membranous outgrowth of hyomandibula in catfishes. A lap joint or sutura limbata is unique to the diplomystids and a sutura harmonica may be found in the trichomycterids. There is no sutural contact between the hyomandibula and metapterygoid in some catfishes such as *Heptapterus, Rhamdia*, and *Parapimelodus* (Figs. 34A, B, 35A), *Loricaria* (Arratia 1990a), and *Pseudeutropius* (Tilak 1964: Fig. 20). In the sisorid *Glyptosternum* (Tilak 1963: Fig. 45), there is a short suture and a ligament between the metapterygoid and hyomandibula, an uncommon condition within siluroids.

The medial part of the metapterygoid may be connected through ligaments to bones of the cranium. For instance: the ligamentous connection between the metapterygoid and parasphenoid, and metapterygoid and posterior part of the vomer is unique to diplomystids (Fig. 19D). The metapterygoid is ligamentously connected to the orbitosphenoid in catfishes such as *Ameiurus* (Fig. 27A) and tachysurids (Tilak 1965: 157). A strong ligament between the metapterygoid and vomer is present in *Galeichthys* and *Bagre marinus*.

Dermo + metapterygoid

The metapterygoid itself does not bear dermal toothplates in teleosts (Jollie 1986); however, the metapterygoid of *Parapimelodus* (Fig. 35B, C) bears a few teeth anteromedially as it does in the 'bagrid' *Chrysichthys brachynemas* (Skelton et al. 1984: Fig. 14A). This bone is therefore not the metapterygoid alone, but the metapterygoid fused with a dermal toothplate. This compound bone is unusual in teleosts, even though Daget (1964) has mentioned it for some. A dermo + metapterygoid is unknown in other 'pimelodids'.

A dermal toothplate is medial to the metapterygoid in the tachysurids *Tachysurus gagora* (Tilak 1965: Fig. 14), *T. serratus*, and *T. thalasinus*. The toothplate is attached by ligaments to the autopalatine and lateral ethmoid according to Tilak (1965: 157), but unfortunately he did not mention whether there is an attachment between the metapterygoid and the toothplate. According to my interpretation, the metapterygoid toothplate — not present in diplomystids, most catfishes or other ostariophysans — is a neoformation as suggested by Tilak (1965). Whether the metapterygoid toothplate is an autapomorphy of *Tachysurus* or a synapomorphy of Tachysuridae has to be demonstrated.

Quadrate-metapterygoid-maxillary ligament

In most catfishes a ligament extends from the quadrate to the metapterygoid and maxilla (e.g., *Noturus*), or the ligament extends only between the quadrate and maxilla (e.g., *Diplomystes*), or the ligament extends only between metapterygoid and maxilla (ligament 5 of Ghiot 1978; e.g., *Pimelodus clarias*), or the ligament is absent (e.g., *Sorubin lima*; Ghiot 1978). A ligament only links the metapterygoid and the maxilla in *Para-*

pimelodus, Bagre, and *Galeichthys* (also *Pimelodus* and *Bagrus* according to Alexander [1965: 106]). The quadrate-metapterygoid-maxillary ligament, or quadrate-maxillary ligament (sometimes quadrate-autopalatine-maxillary ligament), or metapterygoid-maxillary ligament anteriorly bifurcates and each branch inserts on a separate, short articulatory process on the maxilla. I was unable to find a ligament between the maxilla and metapterygoid, or the maxilla and quadrate in *Loricaria*, but there is a ligament between the metapterygoid and premaxilla.

The ligamentum primordiale extends from the lower jaw to the medial side of the maxilla and is usually independent of the metapterygoid-maxillary ligament or the quadrate-metapterygoid-maxillary ligament in siluroids. However, these ligaments may be united such that the ligamentum primordiale in diplomystids inserts on the maxilla, premaxilla, and sometimes on the autopalatine (Arratia 1987a: 25—26, Fig. 7D).

At present, I am unable to evaluate the evolutionary transformations of this ligament that connects the maxilla with the suspensorium, because the information is lacking for most catfishes.

A noteworthy feature of *Galeichthys felis* is an elongate structure, that stains with alcian-blue. It is similar to the central rod within the maxillary barbel; it is attached to the lateral face of the angular (at the coronoid process) and the medial side of the maxilla. This rod lies beside the ligamentum primordiale. I have not seen any similar structures in other catfishes; this structure is anteriorly bifurcate, but it is not attached to the articular processes of the maxilla.

Quadrate and symplectic

In general, two types of quadrate (Fig. 15A, B) are found in catfishes:
1) a simple quadrate that may be present as a small, triangular-shaped bone mainly bearing articular facets (typical of diplomystids); and
2) a complex quadrate that is peculiarly shaped and has an anterior projection that may be of chondral (e.g., *Trichomycterus*; Arratia 1990a) or membranous origin (e.g., *Astroblepus*; Arratia 1990a).

Ontogenetic studies reveal that the enlargement of the complex quadrate and its peculiar shape are acquired through growth.

Catfishes lack the posterior or posteroventral membranous process of the quadrate found in other teleosts. In adults of some ictalurids such as *Ictalurus*, the quadrate (Fig. 41A, B) has a chondral posterior expansion (occupying the position of the membranous posterior process of other teleosts) that sutures to the preopercle.

The presence or absence of a symplectic is open to interpretation. I interpret the cartilage between the hyomandibula and quadrate as the remnant of the symplectic cartilage present early in ontogeny; an ossified symplectic is absent in siluroids. The cartilage has been considered as a remnant of the symplectic or a symplectic cartilage by McMurrich (1884a), Herrick (1901), Kindred (1929), Bhimachar (1933), Skelton (1981), Howes (1983a), and the present paper. This cartilage forms a bridge between the hyomandibula and quadrate. In other teleosts (Arratia & Schultze 1991) the hyomandibula articulates with the symplectic, not the quadrate.
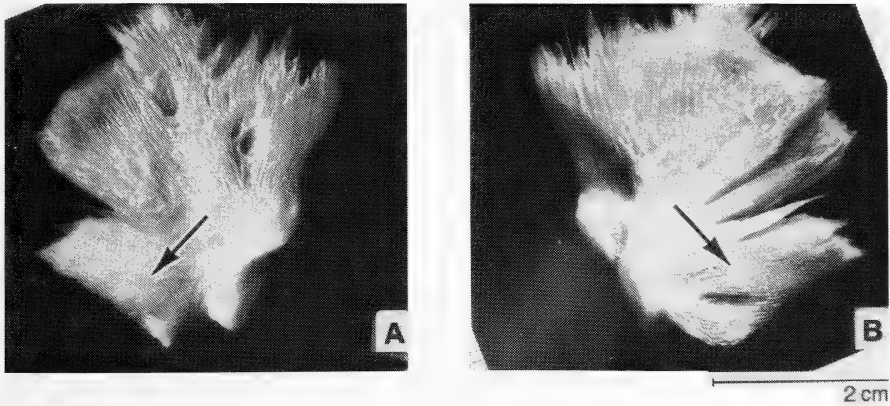
Fig.41: Quadrate of *Ictalurus punctatus* (815 mm standard length; KU 15342). — A: Lateral view; B: Medial view. The chondral posteroventral process of the quadrate is indicated by an arrow.

Ontogenetic studies do not support the loss or fusion of bones (e.g., quadrate and symplectic), but my interpretation has support in the presence of a large cartilaginous symplectic in some diplomystids (Fig. 14A, B) and in *Hypophthalmus* (Howes 1983a: Fig. 23), and in the fusion of the hyo-sympletic and pterygoquadrate early in the ontogeny of siluroids. This fusion produces a special alignment of the hyomandibula and quadrate that is unique to siluroids (Ryder 1887, Kindred 1929, de Beer 1937, Srinivasachar 1956, 1957, 1958a, b, Arratia 1988, 1990a).

An ossified, separate 'symplectic' is present in *Malapterurus* according to Howes (1985: Fig. 13); but this bone occupies a different position and has a unique relationship with the hyomandibula. It is not part of the suspensorium itself, but an ossification lateral to the hyomandibula and quadrate and should not be considered a symplectic.

Hyomandibula

Some of the most interesting features of the hyomandibula include the following features.

1) The presence of a well-developed anterior membranous outgrowth that enlarges during growth. This is an advanced condition within siluroids shared by many catfishes; diplomystids and nematogenyids have a small anterior membranous outgrowth in comparison with siluriforms such as schilbeids and trichomycterids (compare Figs. 17A, 28D, 37A). The anterior membranous outgrowth is rudimentary in 'pimelodids' such as *Heptapterus, Pimelodus, Rhamdia*, and *Parapimelodus* (Figs. 34B, 35A), and in certain 'bagrids' (e.g., *Mystus* and *Rita*; Tilak 1965).

2) The anterior membranous outgrowth of the hyomandibula and the metapterygoid support the eye in some siluroids, including *Eutropiichthys* and *Loricaria*. The eye lies only on the hyomandibula in *Hypostomus*. In primitive catfishes such as diplomystids and nematogenyids, the eye lies on the metapterygoid.

3) A posterior process (Fig. 42B, C) placed between the processus posterodorsalis and opercularis at the posterior margin of the hyomandibula is present in some cat-
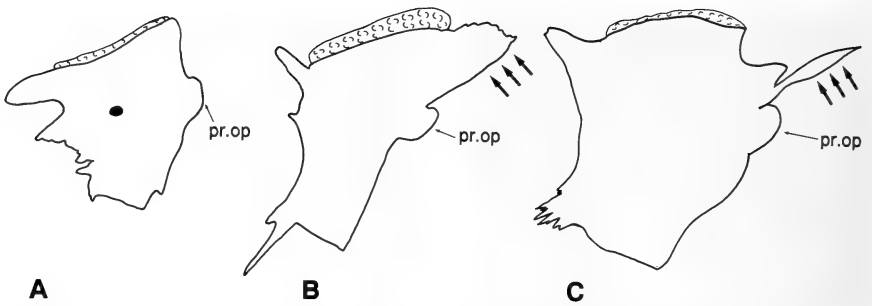
Fig.42: Diagram of hyomandibula. — A: *Diplomystes camposensis*; B: *Rhamdia sapo*; C: *Bagre marinus*. Arrows point to the processus levator operculi.
pr.op: processus opercularis.

fishes. I identify it as the processus levator operculi because it serves as origin site of the levator operculi muscle. It is absent in diplomystids (Figs. 14A, B, 16A—C, 42A), †*Hypsidoris*, and ictalurids, whereas it is broad and ends in a sharp projection in *Nematogenys* (Fig. 28D). It is long in *Heptapterus* and *Rhamdia* (Figs. 34B, 35A, 42B), in *Bagre* (Fig. 42C), and *Arius* (Rao & Lakshmi 1984). In *Nematogenys*, the levator operculi originates on the processus levator operculi of the hyomandibula and on the pterotic; it inserts on the lateral surface of the opercle (Fig. 43B), a unique condition of the family Nematogenyidae according to Howes (1983b). A similar lateral insertion on the opercle is present in *Heptapterus* (Fig. 43C); this condition is autapomorphic to Nematogenyidae and *Heptapterus*. In *Rhamdia* (Fig. 43D) and *Parapimelodus*, the levator operculi originates on the medial aspect of the elongate processus levator operculi of the hyomandibula and inserts on the dorsal and dorsoposterior margin of the medial aspect of the opercle. In diplomystids, the lateral fibers of the levator operculi originate on the dorsoposterior margin of hyomandibula, the pterotic (mainly), and the posttemporo-supracleithrum (Fig. 43A); the insertion of the muscle is as in *Rhamdia*.

4) The position of the opening for the hyoideomandibular nerve trunk has a variety of patterns in adult catfishes and is a feature that needs more attention. The nerve pierces the hyomandibula and then runs lateral to it (Fig. 21A, B) in diplomystids, unlike any other extant siluroid or ostariophysan, where the nerve runs inside the bone. I consider the pattern in diplomystids to be an autapomorphy.

5) The presence or absence of the levator arcus palatini crest and process (that are well-developed in most diplomystids and ictalurids) is another interesting feature that needs attention. This is because it results in change of the insertion of the levator arcus palatini muscle. The muscle has two sections in *Diplomystes camposensis* (Fig. 21C) and *Ictalurus punctatus* (Fig. 26C), whereas it has three sections in *Diplomystes chilensis* (Fig. 21D). The muscle (Fig. 28C) is divided into three sections, almost independent slips, in *Nematogenys*, whereas only one large muscle is present in *Parapimelodus*. The division of the levator arcus palatini muscle was mentioned first by McMurrich (1884b) and later by Winterbottom (1974) for ictalurids. In all of the taxa mentioned above, the insertion of the levator arcus palatini muscle is on
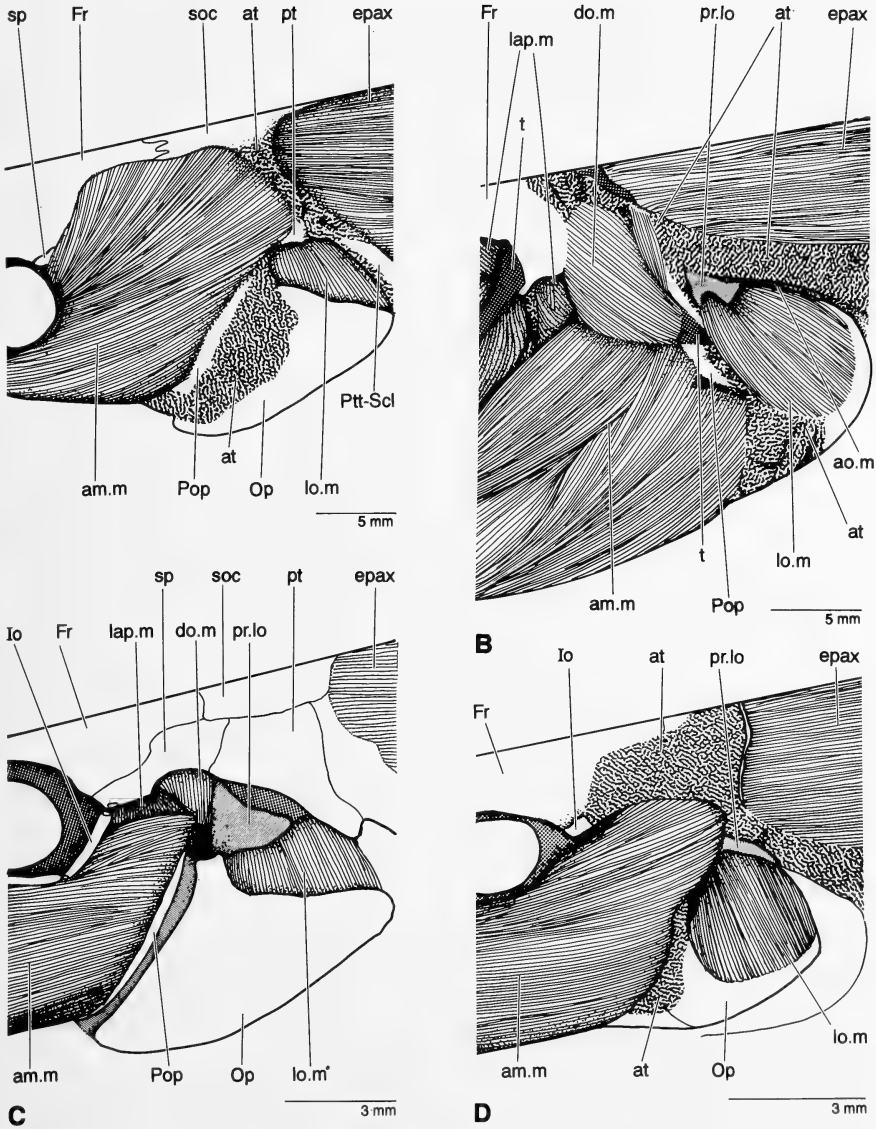
Fig.43: Levator operculi and its relationships in certain catfishes; dorsolateral view of posterior part of head. — A: *Diplomystes camposensis* (PC 220189); B: *Nematogenys inermis* (PC uncat.); C: *Rhamdia sapo* (PC 100285); D: *Heptapterus mustelinus* (PC 147).

at: adipose tissue; am. m: adductor mandibulae; ao. m: adductor operculi; do. m: dilator operculi; epax: epaxialis; Exc: extrascapular; Fr: frontal; Io: infraorbital; lap. m: levator arcus palatini; lo. m: levator operculi; Op: opercle; Pop: preopercle; pr.lo: processus levator operculi; pt: pterotic; Ptt-Scl: posttemporo-supracleithrum; soc: supraoccipital; sp: sphenotic; t: tendon.

the frontal and sphenotic. Although the muscle originates close to the lateral ethmoid in diplomystids, I have not seen the muscle originating on this bone. In *Nematogenys*, the muscle originates at the posterior orbital portion of the frontal and sphenotic; in *Parapimelodus*, the muscle originates mainly or only on the sphenotic.

6) The joint between the hyomandibula and preopercle is variable. Catfishes do not have a preopercular process on the hyomandibula, but the preopercle articulates with the posteroventral margin of the hyomandibula through a harmonic suture (e.g., diplomystids: Fig. 17A), or through a dentate or serrate suture with the posteroventral margin of the hyomandibula (e.g., large ictalurids: Fig. 26C). In some catfishes there is a harmonic suture joining both bones, but dorsally a space remains between them, as in *Eutropiichthys* (Fig. 37A).

7) The cranial bones framing the hyomandibular fossa or facet for the hyomandibula are important to consider (Table 1). The diplomystids are unique in that the processus anterodorsalis of the hyomandibula articulates bone-to-bone with the pterosphenoid and the pterosphenoid forms most the articulation throughout growth. In cypriniforms and gymnotoids only a small section of the pterosphenoid articulates with the hyomandibula, and in this case, through cartilage. In some ictalurids, such as *Ictalurus*, the processus anterodorsalis articulates bone-to-bone with the frontal. In catfishes the autosphenotic and pterotic frame the hyomandibular fossa and this is the common condition (Table 1).

The inclusion of the prootic in the hyomandibular fossa is characteristic of primitive siluroids (Diplomystidae) and some more advanced siluroids (Nematogenyidae and Trichomycteridae) (Table 1). However, in Trichomycteridae the sphenotic is fused with the prootic to form a single element and this element is part of the hyomandibular fossa. In trichomycterids, the pterosphenoid also forms part of the fusion, but is not included in the hyomandibular fossa.

Dermal pterygoids

The reduction in size and number of pterygoids has been considered a specialization of siluroids by McMurrich (1884a), Starks (1926), Nawar (1954), Srinivasachar (1958b), Joseph (1960), and Gosline (1975). As Regan (1911) and Alexander (1965) noted, the ectopterygoid is commonly absent in catfishes, as is the entopterygoid. Pterygoid bones in most catfishes are highly specialized sesamoid elements, connected by ligaments to cranial bones or other bones of the suspensorium; including the metapterygoid and/or autopalatine, or additional bones whose function is unclear (e.g., additional pterygoid in *Parapimelodus*; Fig. 36A).

The bone described here as a dermal ectopterygoid — homologous with that of primitive ostariophysans — is found in some individuals within the Diplomystidae, on one or both sides of the palatal region (Figs. 16A—C, 17A, 19A—D). This small element is ventral to the autopalatine and both bones are attached by connective tissue. It does not articulate with either the entopterygoid or the quadrate, as is generally found in other ostariophysans and teleosts.

Sesamoid 'entopterygoids'

'Entopterygoid' types 1—7 have well-defined ligamentous connections with surrounding bones. For instance, it is common for the catfishes I studied to have a ligament between the metapterygoid and 'entopterygoid' types 1—7 (Fig. 2A—G). In addition, 'entopterygoid' types 1—7 may be joined only to the vomer (types 1—2), or only to the lateral ethmoid (types 3, 5) or to both bones (types 4, 6, 7). It is the common condition of 'entopterygoid' types 2—7 to be linked simultaneously to autopalatine, metapterygoid, and one or more cranial bones (e.g., lateral ethmoid, vomer). A ligamentous connection between the sesamoid 'entopterygoid' and the vomer is not unique to the Diplomystidae as was stated by Alexander (1965), because it is present in other catfishes, including the Nematogenyidae and Ictaluridae. A ligamentous connection between 'entopterygoid' type 1 and the posterior part of the vomer is unique to diplomystids, because in other catfishes the connection is achieved through the anterior part of the vomer (lateral wing) (compare Figs. 19D, 27A—C, 28A, 33).

'Entopterygoid' types 2—7 have a consistent link between the autopalatine and metapterygoid (Fig. 2B—G). The ligamentous connection may be direct, that is from the autopalatine to the 'entopterygoid' and then to the metapterygoid (Fig. 2B—D, G), or it may involve an 'ectopterygoid' type 1 (that appears early in ontogeny as a calcification in the autopalatine-metapterygoid ligament) between the autopalatine and the 'entopterygoid' types 5—6 (e.g., *Bagre*, *Parapimelodus*; Figs. 2E, F, 36A, C). The link is absent in diplomystids.

These data may not appear to be useful when examined separately, but the study of the bones *in situ*, and their relationships with the surrounding bones, reveals the presence of well-defined patterns of suspensoria in catfishes. Fig. 13C shows that diplomystids have a unique pattern of position and relationship of the autopalatine, ectopterygoid, entopterygoid and 'entopterygoid' type 1 (when present). Even though there is intraspecific variation within the family, the absence of the three pterygoids again produces a pattern not found in any other siluroid.

Comparison between 'entopterygoid' types 1—7 described here with those in the literature is difficult, because ligamentous connections have not been commonly mentioned. Nevertheless, I would like to discuss some of the sesamoid 'entopterygoids' described by Tilak (his ectopterygoid). A long, L-shaped entopterygoid ventral to the autopalatine anteriorly and in close contact with the hyomandibula posteriorly, is present in the amblycipitid *Amblyceps mangois* (Tilak 1967: 64, Fig. 2). This 'entopterygoid' occupies a position and has a relationship that differs from entopterygoids types 1—7 (see Terminology); but without knowing its precise ligamentous connections, it is not possible to further define it within the scheme presented here. Gosline (1975: 17) suggested that there was a remote resemblance of this amblycipitid entopterygoid to the bone in sisorids labelled AB in Tilak (1963a: Fig. 42). Bone AB of Tilak does not posteriorly contact the hyomandibula and it may be an additional pterygoid. Moreover, the entopterygoid in *Amblyceps* is dorsally joined by a ligament to the hyomandibula, unlike the catfishes studied here.

The 'entopterygoid' generally does not bear teeth in catfishes; nevertheless, a small, toothed 'entopterygoid' with a ligamentous connection to the metapterygoid is present in the tachysurid *Bactrachocephalus mino* (Tilak 1965: Fig. 13). A large toothed bone anterior to the metapterygoid was figured for *Tachysurus malabaricus* (Tilak 1965: Fig. 12). A large toothed bone with a posterior projection extending close to the quadrate is present in *Osteogeniosus militaris* (Tilak 1965: Fig. 9); and although Tilak (1965) named this bone the ectopterygoid, he recognized (p. 156) that the homology of this bone was not clear and that it could be a displaced autogenous toothed element.

Gosline (1975: 1) concluded that the palatine-maxillary mechanism is represented in modern catfishes by two basal types: that of *Diplomystes* with a toothed maxillary, and that of the 'Bagridae', Ariidae, and several other families in which the 'entopterygoid' forms a movable link between the autopalatine and the posterior part of the suspensorium. The present study reveals that a movable 'entopterygoid' is the most common condition in siluroids and is represented by several patterns, types 2—7 (Fig. 2B—G). In addition to the movable pattern is the immovable type found in large adult ictalurids and 'pimelodids' (e.g., *Rhamdia*), where the 'entopterygoid' becomes sutured to the metapterygoid or to the metapterygoid plus the vomer. The highly specialized pattern of *Trichomycterus* may also be immovable in adults. The determination of the homology of the sesamoid 'entopterygoid' and the dermal entopterygoid is difficult because of the intraspecific variation among the Diplomystidae. I consider the occasional 'entopterygoid' type 1 in *Olivaichthys* to be a new formation not present in other ostariophysans; however, it needs to be confirmed in more individuals before to accept it as an 'entopterygoid'. If this element is a true 'entopterygoid', then, the sesamoid 'entopterygoid' type 1 and the dermal entopterygoid are non-homologous because both pterygoids are present in the same individual. In contrast, 'entopterygoid' types 2—7 are found alone in catfishes without the dermal entopterygoid. According to the distribution of the entopterygoid and 'entopterygoid' (2—7) in ostariophysans, both elements are homologous, because an 'entopterygoid' is present in diplomystids as well as in all probable ancestors of siluroids. I interpret the sesamoid 'entopterygoid' as an evolutionary transformation of the dermal endopterygoid following Ax (1987).

Sesamoid 'ectopterygoid'

A tendon bone ectopterygoid or 'ectopterygoid' type 1 is connected by ligaments to the 'entopterygoid' and to the autopalatine (Figs. 2E, F, 34A, B, 35A, C, 36A) in some 'pimelodids', including *Pimelodus, Parapimelodus, Microglanis, Callophysus, Piramutana*, and *Sciades* (Regan 1911, present paper), in ariids (Regan 1911, Starks 1926, present paper), and in 'bagrids' (Regan 1911, Starks 1926, Jayaram 1966, present paper). A tendon bone 'ectopterygoid' is absent in some 'pimelodids' such as *Rhamdia, Pimelodella, Heptapterus, Hemisorubim, Sorubim*, and *Luciopimelodus* (Regan 1911, Starks 1926, Azpelicueta et al. 1981, present paper).

The tendon bone 'ectopterygoid' type 1 (a calcification within the autopalatine-metapterygoid ligament), which is a sesamoid bone because of its ligamentous connections and function is not homologous with the dermal ectopterygoid present in diplomystids

because a tendon bone 'ectopterygoid' is absent in nematogenyids and ictalurids (see below), and probably in †hypsidorids; therefore, the presence of the 'ectopterygoid' type 1 is a neoformation found in some 'pimelodids', 'bagrids', and ariids.

Opercle and preopercle

I will comment here on the opercular bones, because of their relationship to the suspensorium.

The opercle in trichomycterines has two articulations: the dorsal one with the hyomandibula, and a ventral articulation, where an opercular process or knob fits in a concave articular surface of the preopercle (Arratia 1990b: Fig. 2B). This feature is interesting, because this is a semimovable articulation produced between two dermal bones. This
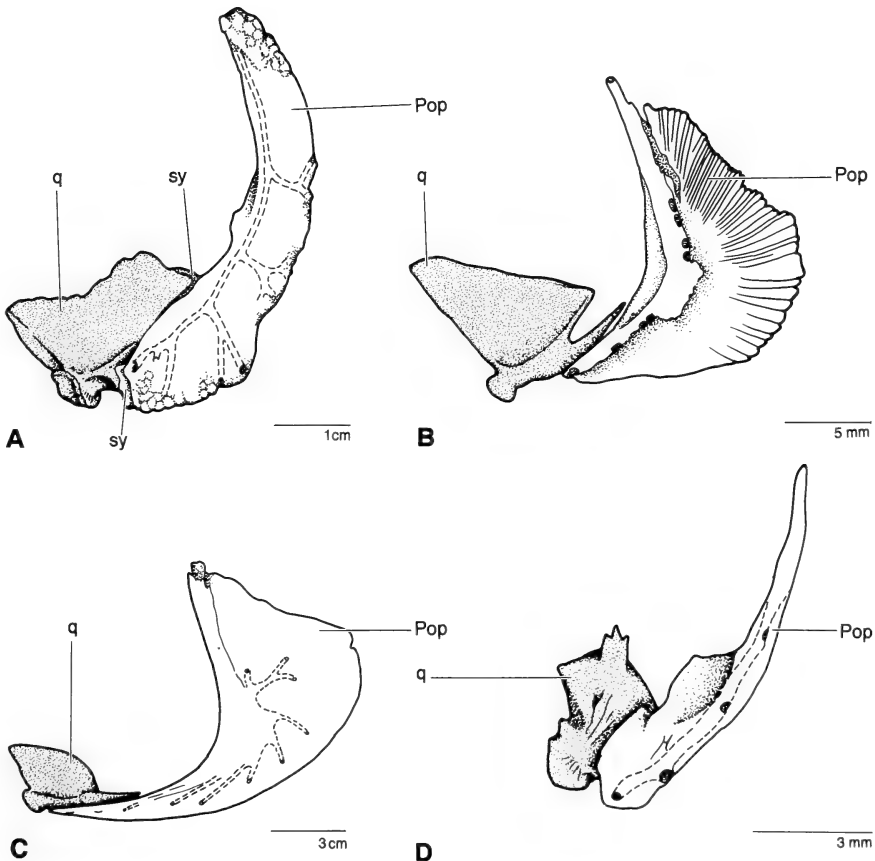
Fig.44: Preopercle and quadrate, lateral view. — A: *Amia calva* (disarticulated specimen; KU 21338); B: *Elops saurus* (225 mm standard length; KU 3053); C: *Chanos chanos* (neurocranium 148 mm in length; CAS-SU 35075); D: *Diplomystes nahuelbutaensis* (disarticulated specimen; BMNH 1867-10-2:22). Pop: preopercle; q: quadrate; sy: symplectic.

implies a modification in the appearance of the dermal bone to produce two articular facets; in some specimens I have even found a small cartilage between the two articular facets. The question is: where is the cartilage derived from? I have not found evidence in young specimens that this cartilage originated in the hyo-symplectic; the only other possible hypothesis is that it is formed during growth from the transformation of connective tissue from the surrounding area.

The preopercle in most siluroids is commonly an elongate dorsoventral structure, mainly carrying the preopercular sensory canal. It has been proposed that catfishes (unlike other teleosts) lack a horizontal limb of the preopercle (Fink & Fink 1981: 321). My comparative studies reveal that the preopercle of primitive catfishes has both the dorsal and ventral limbs and carries the sensory canal just like it does in *Amia* and in other teleosts (Fig. 44A—D). The preopercle of most siluroids has a short ventral limb; in addition, it lacks the posterior or posteroventral outgrowth present in most other teleosts (Fig. 44B, C). In some siluroids, including *Loricaria* and *Ochmacanthus*, it has a short dorsal arm and it does not reach the opercular process of the hyomandibula. It is longer in *Parapimelodus* and *Eutropiichthys* (Figs. 35A, 37A). The ventral part of the siluroids preopercle sutures to the posteroventral articular facet of the simple quadrate or quadrate complex.

The dorsal part of the preopercle may fit in a weakly-defined articular surface in the posteroventral part of the hyomandibula, or both bones may be so closely sutured that it is difficult to separate them in adult catfishes (because of fine bony trabeculae). The sutural relationship between the preopercle and the hyomandibula, symplectic cartilage, and quadrate is a synapomorphy of the catfishes.

COMPARISON AMONG OSTARIOPHYSANS AND THEIR RELATIONSHIPS

The suspensorium of ostariophysans has undergone many evolutionary transformations that provide useful characters at different hierarchic levels. Fink & Fink (1981: 315—321) described 67 synapomorphies amongst the higher levels of ostariophysan relationships. In addition to these, there are several other features of the suspensorium that characterize ostariophysans and are analyzed below.

A combined outgroup that includes elopomorphs, clupeomorphs, and escoids have been used here as an outgroup to polarize characters. The numbers of the characters shown in the cladograms in Fig. 45A and B and Appendix 1 correspond to those below. Characters 39 to 131 are from Fink & Fink (1981) and correspond to characters outside the suspensorium.

C h a r a c t e r 1. The cartilaginous palatoquadrate visible early in ontogeny is lateral to the dorsal portion of the hyoid arch (hyo-symplectic) in ostariophysans and other teleosts except for the catfishes and gymnotoids (Arratia 1988, 1990a, present paper, Arratia & Schultze 1991). In catfishes the posterior part of the palatoquadrate is fused with the hyoid arch, whereas in gymnotoids the posterior part of the palatoquadrate

is medial to the dorsal limb of the hyoid arch. Although I have coded these conditions as 1 and 2 (Appendix 1), their polarity is unknown; e.g., it is unclear whether the placement of the palatoquadrate medial to the hyo-symplectic is more primitive than the fused elements in catfishes, or whether both conditions have evolved directly from the primitive stage. Character 1[1] might be a synapomorphy of gymnotoids, or possibly of siluriforms, whereas character 1[2] is a synapomorphy of catfishes.

1) Palatoquadrate:
    0: lateral to hyo-symplectic cartilage
    1: medial to hyo-symplectic cartilage
    2: fused with hyo-symplectic cartilage

C h a r a c t e r 2. A single, elongate palatoquadrate (Figs. 3, 4A, B, 8A) is characteristic of ostariophysans and other actinopterygians except for catfishes. In catfishes, the palatoquadrate has a separate pars autopalatina (Figs. 24A—D, 46A—C; Arratia 1988, 1990a, Arratia & Schultze 1991).

2) Palatoquadrate:
    0: as a single unit
    1: pars autopalatina separate from the pars pterygoquadrata

C h a r a c t e r 3. In ostariophysans as well as in other actinopterygians, the posterior part of the palatoquadrate is not fused to the dorsal part of the hyoid arch. In catfishes both parts are fused, forming the hyo-symplectic-pterygoquadrate plate (Figs. 24A—D, 46A—C; de Beer 1937, Srinivasachar 1956, 1957, 1958a, b, Arratia 1988, 1990a, Arratia & Schultze 1991).

3) Posterior part of palatoquadrate:
    0: not fused with hyo-symplectic cartilage
    1: fused with hyo-symplectic cartilage

C h a r a c t e r 4 and 5. The posterodorsal part of the palatoquadrate is simple in primitive ostariophysans as well as in other teleosts; however, it is bifid in cypriniforms and characiforms. Within the ostariophysans, cypriniforms and characiforms share a posteriorly bifurcate pterygoquadrate early in ontogeny; this feature may be or may not be retained in adults (Figs. 8A—B, 10A; Arratia & Schultze 1991: Fig. 28A—E). According to Fink & Fink (1981: their characters 26 and 30) "in otophysans the endochondral portion of the metapterygoid is an axe-shaped bone, either double headed (most cypriniforms and characiforms), or single headed, with the posterior half of the bone absent (siluriforms)." I have not found ontogenetic evidence to support this character — that the posterior part of the metapterygoid is absent in Siluriformes, sensu Fink & Fink (1981). The metapterygoid of diplomystids and other primitive catfishes has the same notch separating the processus basalis from the posterior part of the early metapterygoid (similar to the metapterygoid early in ontogeny of other primitive ostariophysans and other teleosts and *Amia*; see Arratia & Schultze 1991). The metapterygoid of gymnotoids, however, is a small triangular bone lacking the processus basalis, the notch, and the posterior part that joins the hyomandibula and cartilage between hyomandibula and symplectic. I therefore consider that this character is not a synapomorphy of gymnotoids and catfishes, but a gymnotoid autapomorphy.

Fink & Fink (1981) also state that "In siluriforms the endochondral portion of the metapterygoid is triangular and appears to be equivalent to the anterior half of the metapterygoid in primitive otophysans" (their character 31). I am unable to find support for this character because the ontogeny of the fishes do not support it. The metapterygoid of diplomystids not only has a triangular-shaped endochondral portion; in addition, the triangular endochondral portion in gymnotoids is just the opposite (it extends posteriorly) of that illustrated for *Diplomystes* by Fink & Fink (1981: compare Figs. 11, 12) and herein (Figs. 12A, B, 17A, 18C).

  4) Posterodorsal portion of the palatoquadrate (in young individuals and some adults):
    0: smooth
    1: bifid
    2: fused to the hyoid arch

When this character is run in the PAUP program as unordered, the result is that character-state 1 appears in parallel in Cypriniformes and Characiformes; when the character is ordered, the program interprets it as an otophysan synapomorphy, that has a reversal (4[0]) in gymnotoids. When character-state 2 is replaced by "?", the PAUP program interprets 4[0] as a synapomorphy of siluriforms.

  5) Small, triangular chondral metapterygoid lacking notch and processus basalis:
    0: absent
    1: present

C h a r a c t e r 6. Fink & Fink (1981) state that "In gonorynchiforms the suspensorium is elongate in a parasagittal plane in the region between the articular condyle for the quadrate and the hyomandibula" (their character 29). (This is however, not the articular condyle for the quadrate; it is for the lower jaw.) Although this character was considered by them to be an autapomorphy of the gonorynchiforms, a parasagittal elongation of suspensorium between the articular condyle of the quadrate and hyomandibula is not unique to gonorynchiforms among the ostariophysans. This is because parasagittal elongation is also present in the primitive *Xenocharax*. However, in these two cases, each is independently derived (compare Figs. 4D, 10A). In gonorynchiforms the parasagittal elongation is due to the separation between the quadrate and symplectic, whereas in *Xenocharax* the elongate symplectic is almost parallel to the long axis of the body and is medial to the quadrate. I propose to modify this character as follows:

  6) Parasagittal elongation of suspensorium due to separation between the quadrate and symplectic:
    0: absent
    1: present

This character is only present in gonorynchiforms, among ostariophysans, and it is not found in other primitive teleosts — therefore it is a gonorynchiform autapomorphy.

C h a r a c t e r 7. A bony autopalatine is present in ostariophysans, but not in gymnotoids (compare Figs. 4D, 8B, 10A, 12A, B, 17A). In the latter, the pars autopalatina is still present in most adult gymnotoids; however, some gymnotoids exhibit chon-

droidal osteogenesis in the pars autopalatina and therefore only a chondroidal auto-palatine is formed (Fig. 12B—D).

7) Bony autopalatine:
    0: present
    1: absent

C h a r a c t e r 8. A dermopalatine is absent in ostariophysans. Toothplate(s) associat-ed with the autopalatine are found in certain catfishes (see below).

8) Dermopalatine:
    0: present
    1: absent

C h a r a c t e r 9. In ostariophysans as well as other teleosts, the autopalatine articu-lates with one or more cranial elements; however, a cranial articulation — either direct or indirect via cartilage — is missing in gymnotoids, even in those forms with a chon-droidal autopalatine.

9) Autopalatine articulates with neurocranium through cartilage or directly:
    0: present
    1: absent

C h a r a c t e r 10. The anterior cartilage of the autopalatine contacts the meseth-moidal-vomerine region throughout an intermediate cartilaginous, fibrocartilaginous, or chondroidal element in ostariophysans, with the exception of the catfishes and the gymnotoids.

10) Anterior cartilage of autopalatine, or pars autopalatina, or chondroidal auto-palatine has a direct or indirect contact with neurocranium:
    0: present
    1: absent

C h a r a c t e r 11. The autopalatine may articulate indirectly with the vomer as it does in ostariophysans. The autopalatine and vomer articulate indirectly through cartilage or fibrocartilage in primitive gonorynchiforms, characiforms, and catfishes. In diplo-mystids there is a large surface that articulates with the cartilage contacting the vomer (mainly), and also the lateral ethmoid, mesethmoid, and orbitosphenoid (Figs. 16B, C, 19B, C). A chondroidal element connects the autopalatine and vomer in adult cypriniforms. No articulation is present in gymnotoids.

11) Autopalatine and vomer:
    0: articulate indirectly through cartilage or fibrocartilage
    1: articulate indirectly through a chondroidal element between the mesethmoid and vomer (character 4 by Fink & Fink 1981)
    2: do not articulate with each other

C h a r a c t e r 12. The location of the articulation between the autopalatine and vomer differs among ostariophysans. The anterior cartilage or fibrocartilage of the autopalatine (Fig. 6A—D) articulates either directly or indirectly with the vomer in ostariophysans, with the exception of catfishes and gymnotoids. However, the condi-tion differs in both groups. In catfishes, the articulation between the autopalatine and vomer is near the midpoint of the length of the autopalatine; in gymnotoids, there is

no articulation between the pars autopalatina or the chondroidal autopalatine and vomer.

    12) Vomerine articular surface on autopalatine:
        0: placed anteriorly
        1: placed at midlength of the autopalatine
        2: no articulation present

When this character is run unordered, the PAUP program interprets 12[1] as a synapomorphy of catfishes and 12[2] as a synapomorphy of gymnotoids. When the character is ordered, the PAUP interprets 12[1] as a synapomorphy of siluriforms. When character-state 2 is replaced by "?", the PAUP program interprets 12[1] as a synapomorphy of siluriforms.

C h a r a c t e r 13 and 14. The autopalatine articulates with the lateral ethmoid in cypriniforms, characiforms, and catfishes. Neither the pars autopalatina or the chondroidal autopalatine articulates with the lateral ethmoid in gymnotoids. Gonorynchiforms resemble primitive teleosts such as elopomorphs (Arratia & Schultze 1991: Fig. 35D, E) and osteoglossomorphs (without autopalatine; Arratia & Schultze 1991: Fig. 20A, B) in the lack of this articulation. However, part of the outgroup — the clupeomorphs and the esocoids — present the articulation. Considering that the closer outgroup has the articulation, I consider its presence as the primitive condition. Therefore, I interpret the absence of the articulation between autopalatine and lateral ethmoid as an autapomorphy of the gonorynchiforms. There are also differences in the location of the articular facet for the lateral ethmoid on the autopalatine (Fig. 6B—D). For instance, it is on the posterior cartilage of the autopalatine in *Xenocharax*, but on the medial surface of the small autopalatine in *Hoplias* (Fig. 11). It is closer to the posterior cartilage of the autopalatine than to the midlength in cypriniforms. It is at about the midlength of the bone or slightly anterior to it in catfishes.

    13) Autopalatal articulation with lateral ethmoid:
        0: present
        1: absent
        2: neither pars autopalatina or chondroidal autopalatine articulate with lateral ethmoid

There is no difference when the character is run ordered or unordered in the PAUP program. Character 13[1] is a gonorynchiform synapomorphy and 13[2] a gymnotoid synapomorphy. When character-state 2 is replaced by "?", the PAUP program interprets 13[1] as a gonorynchiform synapomorphy.

    14) Articulation between the autopalatine and lateral ethmoid near the midlength of the autopalatine:
        0: absent
        1: present

This character is a synapomorphy of catfishes at the primitive level; several advanced catfishes lack this feature (e.g., Taverne & Aloulou-Triki 1974, Arratia 1990a).

C h a r a c t e r 15. A single articular facet for the autopalatine or for a maxillary-autopalatal cartilage is present on the maxilla of ostariophysans, with the exception of

catfishes. In primitive catfishes, two large articular facets on the maxilla articulate with the anterior cartilage(s) of the autopalatine (Figs. 18A, B, 19A—C).

15) Maxilla with two articular facets for autopalatine:
    0: absent
    1: present

C h a r a c t e r 16. Fink & Fink (1981) state that "In siluriforms, a ligament extends between the maxilla adjacent to its articulation with the palatine and the dorsal tip of the lower jaw" (their character 45). The ligamentum primordiale in diplomystids extends between the maxilla (premaxilla and/or autopalatine, occasionally) (Arratia 1987a: Fig. 7A—C) and the coronoid cartilage of the lower jaw, not on the angular portion of the angulo-articulo-retroarticular. The gymnotoids examined here do not have a coronoid cartilage in the lower jaw and the insertion is between the maxilla and the bony dorsal tip of the coronoid process of the lower jaw.

16) Ligamentum primordiale connects the dorsal tip of the lower jaw with the maxilla:
    0: absent
    1: present

C h a r a c t e r 17. Fink & Fink (1981) state that, "In cypriniforms the anterior portion of the palatine has a dorsomedial process which abuts against the mesethmoid" (their character 21). The processus dorsomedialis mainly abuts the lateral portions of the vomer in primitive cypriniforms and a short ligament connects this process and the mesethmoid. I therefore modify the character by Fink & Fink (1981) as follows:

17) Processus dorsomedialis of autopalatine ligamentously attached to mesethmoid:
    0: absent
    1: present

C h a r a c t e r 18. Fink & Fink (1981), following previous researchers state that "In cypriniforms the palatine articulates posteriorly in a concave facet on the mesopterygoid." (Swinnerton 1902, Starks 1926, Ramaswami 1955a, 1955b, 1957, Roberts 1973, Gosline 1975, Fink & Fink 1981: their character 22). The posterior cartilage of the autopalatine articulates with the entopterygoid in the Diplomystidae and with the 'entopterygoid' type 2 in the Nematogenyidae. This differs from the cypriniforms in the mobility of the bones. In cypriniforms the articulation is semimovable, and the autopalatine is able to move in relation to the concave articular facet of the entopterygoid, and both bones are linked by a short ligament. In primitive catfishes, the entopterygoid or 'entopterygoid' type 2 are closely attached to the autopalatine and both bones are not able to move in relation to each other.

18) Semimovable articulation between the posterior cartilage of the autopalatine and a concave facet of the entopterygoid:
    0: absent
    1: present

C h a r a c t e r 19. Fink & Fink (1981) state that, "In cypriniforms, the ectopterygoid does not overlap the palatine anteriorly, permitting mobility of the palatine relative to the rest of the suspensorium" (their character 25). It is true that the ectopterygoid does

not reach the autopalatine in cypriniforms; instead, a ligament links both bones, and the autopalatine is mobile. However, in the characiform *Xenocharax* (CAS-SU 15639), there is a loose connection between the ectopterygoid and autopalatine, and the latter is mobile relative to the rest of the suspensorium; a situation not observed in *Hoplias* and other characiforms studied herein (not in *Xenocharax* specimens studied by S. Fink, in litteris). At this time, I therefore suggest changing this character as follows:

   19) The ectopterygoid does not extend ventrally to the autopalatine nor does it suture with the autopalatine:
   0: absent
   1: present

C h a r a c t e r 20. Fink & Fink (1981) state that, "In siluriforms the ectopterygoid is greatly reduced posteriorly (siluroids) or absent (gymnotoids)" (their character 26). This character is correct in part; I would like to point out that it is true only for diplomystids among the siluroids, which may have a small ectopterygoid or lack the ectopterygoid entirely. In most catfishes the ectopterygoid is absent. A few catfishes present an 'ectopterygoid'.

   20) Ectopterygoid:
   0: well developed
   1: rudimentary or absent

C h a r a c t e r 21. Fink & Fink (1981) state the following, "In siluroids the mesoptery-goid is reduced to a small plate of bone posteromedial to the posterior tip of the palatine and is not in contact with the posterior portion of the suspensorium" (their character 27). This statement is, maybe, only true for diplomystids among the catfishes; an 'entopterygoid' is present in the other catfishes studied here. In other ostario-physans, as well as in other teleosts, the entopterygoid is a moderately large plate of bone articulating with the autopalatine, metapterygoid, and quadrate posteriorly (Figs. 4D, 8B, 10A).

   21) Entopterygoid small, reduced to a small cup-like bone near the posterior cartilage of the autopalatine:
   0: absent
   1: present

C h a r a c t e r 22. Fink & Fink (1981) also say that, "In gymnotoids the mesopterygoid has a vertical strut which usually articulates with the orbitosphenoid" (their character 28). The dorsomedial (Fig. 12A, B) process of the entopterygoid of gymnotoids may articulate with the orbitosphenoid as well as the cartilage between the orbitosphenoid and lateral ethmoid, or with all three elements together (e.g., adult *Gymnotus carapo*). The dorsomedial process of the entopterygoid is not present in other teleosts.

   22) Entopterygoid with a vertical dorsomedial process:
   0: absent
   1: present

C h a r a c t e r 23. The entopterygoid is the sole or the main support of the eye in most teleosts (Arratia & Schultze 1991); however the condition differs in catfishes, where the

metapterygoid, the metapterygoid and the hyomandibula, or the hyomandibula alone may support the eye.

23) Entopterygoid is the main support of the eye:
    0: present
    1: absent

C h a r a c t e r 24. Fink & Fink (1981) state that "In siluroids the metapterygoid is situated anterodorsal to the quadrate and forms part of the ventral border of the suspensorium (Fig. 11). In other ostariophysans and primitive teleosts, the metaptery-goid is posterodorsal to the quadrate" (their character 32).

24) Metapterygoid anterodorsal to quadrate and forms part of the ventrolateral border of the suspensorium:
    0: absent
    1: present

C h a r a c t e r 25 and 26. In the Gymnotoidei the metapterygoid (Fig. 12A, B) is at least medial to (in some species) and partially overlapped by the hyo-symplectic, a position which is retained in adults (e.g., *Sternopygus* in Fink & Fink 1981, Mago-Lecía et al. 1985: Fig. 3; and personal observation for *Gymnotus* and *Hypopomus*). This condition found in gymnotoids appears to be a unique feature of the group within the ostariophysans. In gymnotoids a ligament extends between the metapterygoid and posterior ceratohyal. A similar ligament is not found in other primitive ostariophysans and primitive teleosts.

25) Metapterygoid-posterior ceratohyal ligament:
    0: absent
    1: present

26) Posterior margin of the metapterygoid medial to hyomandibula:
    0: absent
    1: present

C h a r a c t e r 27. In primitive siluroids the posterior margin of the metapterygoid is both sutured (dentata and/or serrata) and synchondrally articulates with the hyoman-dibula and quadrate (Figs. 17A, 22D). In most ostariophysans the posterior margin of the metapterygoid only articulates with the anteroventral part of the hyomandibula and the cartilage between the hyomandibula and symplectic (Figs. 4D, 8B, 10A); often the metapterygoid overlaps the hyomandibula producing a lap joint.

27) Posterior margin of metapterygoid sutured to hyomandibula and quadrate:
    0: absent
    1: present

C h a r a c t e r 28. A membranous posteroventral process of the quadrate is present in most teleosts; this process is absent in siluroids.

28) Posteroventral process of quadrate:
    0: present
    1: absent

C h a r a c t e r 29. In most teleosts the quadrate and hyomandibula are attached by connective tissue to the preopercle, whereas they are sutured in siluroids. Quadrate and

hyomandibula are sutured to preopercle by a sutura harmonica in diplomystids (Fig. 17A) and nematogenyids (Fig. 28D), however sutura dentata and serrata are found in other catfishes (Figs. 22D, 26C, 33C, 34B). A combination of both sutura harmonica and sutura serrata is present in certain catfishes (e.g., *Synodontis*: Taverne & Aloulou-Triki 1974: Fig. 39).

29) Quadrate and hyomandibula are sutured to preopercle:
0: absent
1: present

C h a r a c t e r 30. A metapterygoid-quadrate fenestra (Fig. 8B) is present in primitive cypriniforms such as *Opsariichthys* and *Zacco* and most characiforms. A quadrate-metapterygoid fenestra is absent in other ostariophysans.

30) Metapterygoid-quadrate fenestra:
0: absent
1: present

A metapterygoid-quadrate fenestra is shared by cypriniforms (at least in the primitive members) and characiforms; nevertheless the clupeomorph *Brevoortia* has also this fenestra (Gosline 1973) and also, a posteriorly bifurcated pterygoquadrate early in ontogeny. Gosline (1973) considered the metapterygoid-quadrate fenestra to be independently acquired in cypriniforms and characiforms by citing its presence in *Brevoortia*. Fink & Fink (1981: 320) considered the fenestra to be an otophysan character.

C h a r a c t e r 31. A well-ossified, slightly triangular symplectic bone is present in ostariophysans and other teleosts except siluroids.

31) Symplectic bone:
0: present
1: absent

C h a r a c t e r 32. The hyomandibula may articulate through one or two articular facets with the neurocranium (see Table 1).

32) Hyomandibula articulates with neurocranium through:
0: a double articular facet
1: a single articular facet

C h a r a c t e r 33. The hyomandibula does not articulate with the pterosphenoid in most ostariophysans except the catfishes and gymnotoids (Table 1). However, the pterosphenoid and anterior part of the hyomandibula articulate bone-to-bone in diplomystids (an autapomorphy of Diplomystidae according to Arratia 1987) and a synchondral articulation between both bones is present in gymnotoids.

33) Pterosphenoid:
0: not articulating with hyomandibula
1: articulates bone-to-bone with hyomandibula
2: synchondrally articulates with hyomandibula

When the character is unordered, the PAUP program interprets 33[1] as a siluroid synapomorphy and 33[2] as a gymnotoid synapomorphy. When the character is ordered, 33[1] is interpreted as a siluriform synapomorphy.

C h a r a c t e r 34. In most ostariophysans and other primitive teleosts the interhyal articulates with the cartilaginous region between the hyomandibula and symplectic. A small interhyal is present in certain catfishes such as diplomystids and nematogenyids, but it is absent in others (Arratia 1990a). However, in primitive siluroids the proximal part of the small interhyal does not articulate with the dorsal part of the hyoid arch and a ligament extends between the posterior ceratohyal and the hyomandibula (Arratia 1990a). A ligament connects both bones in catfishes without an interhyal.

    34) Interhyal:

        0: articulating proximally with the cartilaginous region between hyomandibula and symplectic

        1: proximal articulation lost; a ligament joins the posterior ceratohyal and hyomandibula

C h a r a c t e r 35. In gymnotoids the quadrate articulates with both the articular and the retroarticular when the mouth is closed; in other ostariophysans the retroarticular is not included in the articular facet. The retroarticular excluded from the quadrate-mandibular joint is a character present in most clupeocephalans; however, among the combined outgroup, the retroarticular is included in the quadrate-mandibular joint in elopomorphs and osteoglossomorphs (Nelson 1973, Patterson & Rosen 1977, Arratia 1987b). I consider the absence of the retroarticular from this joint as the primitive condition by comparison to the clupeocephalans.

    35) Quadrate articulates with articular and retroarticular when mouth closed:

        0: absent

        1: present

C h a r a c t e r 36. The retroarticular is a separate bone in the lower jaw of ostariophysans (Figs. 8C, 10C, D, 12E, F). However in catfishes the retroarticular is fused early in ontogeny to a well-developed articular and a small angular producing a compound element, the angulo-articulo-retroarticular (Fig. 20A, B). The retroarticular is partially fused to the angulo-articular in a large specimen of *Chanos chanos* examined here (CAS-SU 35075).

    36) Retroarticular as separate ossification in adult individuals:

        0: present

        1: absent

C h a r a c t e r 37. The Meckelian cartilage is an elongate cartilage — tube-like — in most teleosts. However it projects dorsally in siluroids, forming the coronoid process of the Meckelian cartilage, which is medial to the dorsal projections of the dentary and angular. A well-developed coronoid cartilage is present in the early ontogeny of catfishes and it is retained in adult primitive siluroids such as diplomystids (Figs. 20A, B; Arratia 1987a: Figs. 7A—C, 26A, B, F).

    37) A well developed dorsal projection — coronoid process — of the Meckelian cartilage:

        0: absent

        1: present

Characters 38 to 130 correspond to characters taken from Fink & Fink (1981). When a character is modified, it is explained in the text.

C h a r a c t e r 38. Kinethmoid bone attached by ligaments to the anterodorsal margin of the mesethmoid and to the premaxillary ascending process (Fig. 5B; Arratia & Schultze 1991: Fig. 30A):
> 0: absent
> 1: present

C h a r a c t e r 39. Vomer articulated anteriorly with mesethmoid (Fink & Fink 1981: Fig. 4):
> 0: absent
> 1: present

C h a r a c t e r 40. Anteroventral processes of the mesethmoid articulated directly with premaxillae (Figs. 5A—C, 19A—C; Fink & Fink 1981: Fig. 3C—F):
> 0: absent
> 1: present

C h a r a c t e r 41. Compressed dorsal portion of the mesethmoid that appears slender from dorsal aspect:
> 0: absent
> 1: present

C h a r a c t e r 42. Bone and cartilage of interorbital septum greatly reduced:
> 0: absent
> 1: present

C h a r a c t e r 43. Basisphenoid:
> 0: present
> 1: absent

C h a r a c t e r 44. Sacculi and lagenae situated more posteriorly and nearer the midline than in other primitive teleosts (Rosen & Greenwood 1970):
> 0: absent
> 1: present

C h a r a c t e r 45. Foramen on the ventral face of the prootic through which the utricular otolith is visible (Weitzman 1962: Fig. 4):
> 0: absent
> 1: present

C h a r a c t e r 46. Separate ossifications of the parietals are present from early ontogeny in the outgroup. However, separate parietals are absent in adult siluroids; a single bone occupies the position of parietals plus supraoccipital in other teleosts. This character is modified from the original description by Fink & Fink (1981).
> 46) Parietals as separate ossifications from early in ontogeny:
> 0: present
> 1: absent

C h a r a c t e r 47. Dorsomedial opening into posttemporal fossa (Fink & Fink 1981: Fig. 5C):

    0: absent

    1: present

C h a r a c t e r 48. Intercalar:

    0: present

    1: absent

C h a r a c t e r 49. An exoccipital or exoccipital and supraoccipital with a prominent posterodorsal cartilaginous margin framing the foramen magnum is present in young primitive gonorynchiforms; the cartilaginous margin is comparatively smaller in large individuals.

    49) Exoccipitals or exoccipitals and supraoccipital with a prominent posterodorsal cartilaginous margin framing the foramen magnum:

    0: absent

    1: present

C h a r a c t e r 50. Large, globular lagenar capsule projecting well lateral to the cranial condyle:

    0: absent

    1: present

C h a r a c t e r 51. Sclerotic bones:

    0: present

    1: absent

C h a r a c t e r 52. In primitive catfishes and gymnotoids the infraorbital series is mainly formed by the infraorbital canal-bearing portions of the bones. In certain advanced siluriforms, the infraorbital may be slightly expanded.

    52) Primitively, infraorbital series formed largely or entirely of canal-bearing portions of bones:

    0: absent

    1: present

C h a r a c t e r 53. A dermal supraorbital bone is present in most members of the outgroup and in primitive ostariophysans. A dermal supraorbital bone is absent in siluriforms. In certain advanced catfishes such as trichomycterids, a tendon bone supraorbital forms early in ontogeny as an ossification of the ligament connecting the frontal with infraorbital bones. This element is not homologous with the dermal supraorbital, and it is considered herein as a new formation. The character by Fink & Fink (1981) is modified as follows:

    53) A dermal supraorbital bone:

    0: absent

    1: present

C h a r a c t e r 54. Subopercle:

    0: absent

    1: present

C h a r a c t e r 55. An opercle approximately triangular-shaped is present in primitive catfishes and in numerous advanced ones. In contrast, the shape of the opercle is highly modified in certain catfishes such as the trichomycterids.

55) Primitively, opercle approximately triangular in shape rather than approximately rectangular:
> 0: absent
> 1: present

C h a r a c t e r 56. Premaxillae extend furthest dorsally adjacent to the midline (Fig. 5B; Fink & Fink 1981: Fig 3B):
> 0: absent
> 1: present

C h a r a c t e r 57. Very thin, flat premaxilla:
> 0: absent
> 1: present

C h a r a c t e r 58. Maxilla posterolateral to lateral processes of mesethmoid and not articulating directly with mesethmoid (Figs. 5C, D, 19A—C; Fink & Fink 1981: Fig. 3C—F):
> 0: absent
> 1: present

C h a r a c t e r 59. As Fink & Fink (1981) noted, the maxillary barbel in primitive cypriniforms is at the rictus of the mouth and may or may not be closely associated with the tip of the maxilla. All siluroids have a maxillary barbel that has a central rod of a substance that stains with alcian blue, but whose structure and composition are still unclear and vary among catfish groups (see Arratia 1987a, for literature on the subject). The maxillary central rod is proximally expanded and forms a support plate that is medial to the maxilla. The barbels of cypriniforms and siluroids are interpreted to have evolved independently.

59) Maxillary barbel:
> 0: absent
> 1: present

C h a r a c t e r 60. Supramaxilla:
> 0: present
> 1: absent

C h a r a c t e r 61. Teeth in the jaws:
> 0: present
> 1: absent

C h a r a c t e r 62. Replacement teeth for outer row dentary teeth and some premaxillary teeth formed in trench or crypts in the bone:
> 0: absent
> 1: present

C h a r a c t e r 63. "Epibranchial organ":
> 0: absent
> 1: present

Character 64. Teeth on the second and third pharyngobranchial and basihyal are present in primitive teleosts and in characiforms among ostariophysans. A basihyal is absent in catfishes, therefore the character by Fink & Fink (1981) is modified as follows:

64) Teeth from second and third pharyngobranchials and basihyal, when the last is present:
0: present
1: absent

Character 65. Two posterior pharyngobranchial toothplates:
0: present
1: absent

Character 66. Teeth on the fifth ceratobranchial:
0: present
1: absent

Character 67. Toothplates associated with basibranchials 1—3:
0: present
1: absent

Character 68. One pharyngobranchial toothplate:
0: absent
1: present

Character 69. Fifth ceratobranchial enlarged, extending much dorsally than the other ceratobranchials:
0: absent
1: present

Character 70. Teeth on the fifth ceratobranchial ankylosed to the bone:
0: absent
1: present

Character 71. Gasbladder divided into a smaller anterior and larger posterior chamber, with the ductus pneumaticus near the constriction (Rosen & Greenwood 1970):
0: absent
1: present

Character 72. Anterior chamber of gasbladder partially or completely covered by a silvery peritoneal tunic:
0: absent
1: present

Character 73. Peritoneal tunic of anterior chamber of the gasbladder attached to the anteriormost two pleural ribs (Rosen & Greenwood 1970):
0: absent
1: present

Character 74. Dorsal mesentery suspending the gasbladder heavily thickened anterodorsally near its attachment to the vertebral column and with many transverse fibers:

0: absent

1: present

C h a r a c t e r 75. Expanded dorsomedial portions of anterior neural arches that abut against each other and the posterior margin of the exoccipital, forming a roof over the neural canal:

0: absent

1: present

C h a r a c t e r 76. Neural arch anterior to the arch of the first vertebral centrum:

0: present

1: absent

C h a r a c t e r 77. Anterior neural arch especially enlarged and with an extensive, tight joint with the exoccipital or exoccipital and supraoccipital:

0: absent

1: present

C h a r a c t e r 78. Scaphium as a modification of the first neural arch:

0: absent

1: present

C h a r a c t e r 79. Ossified claustrum:

0: absent

1: present

C h a r a c t e r 80. The scaphium extends well anterior to the border of centrum 1:

0: absent

1: present

C h a r a c t e r 81. Second neural arch modified to form the intercalarium:

0: absent

1: present

C h a r a c t e r 82. Third neural arch with an elongate anterodorsal process which projects lateral to the ascending process of the intercalarium:

0: absent

1: present

C h a r a c t e r 83. Anterior margin of the third neural arch approaches closely the posterior border of the neurocranium:

0: absent

1: present

C h a r a c t e r 84. Dorsal part of the third neural arch with a distinct, short anterior margin which is vertical in orientation:

0: absent

1: present

C h a r a c t e r 85. Anteroventral process of the third neural arch articulated or fused to a dorsal prominence on the second centrum:

0: absent

1: present

C h a r a c t e r 86. Third and fourth neural arches fused together and to the complex centrum:
    0: absent
    1: present

C h a r a c t e r 87. Fifth neural arch fused to its centrum:
    0: absent
    1: present

C h a r a c t e r 88. Three anterior vertebrae foreshortened, with the anterior centrum being especially foreshortened, the second less so, and the third slightly less again:
    0: absent
    1: present

C h a r a c t e r 89. Centra 2—4 fuse into a complex centrum in primitive catfishes (diplomystids); the fifth or more posterior centra are added to the fusion in other catfishes.
    89) Centra 2—4 fused into a complex centrum:
    0: absent
    1: present

C h a r a c t e r 90. The anteriormost parapophyses may be present in the outgroup or absent; when they are present, they are autogenous.
    90) Anteriormost two parapophyses, when present, fused to the centra:
    0: absent
    1: present

C h a r a c t e r 91. Parapophysis, fused or autogenous, on the anterior centrum:
    0: present
    1: absent

C h a r a c t e r 92. Parapophysis of the second centrum:
    0: present
    1: absent

C h a r a c t e r 93. Elongate lateral process of the second centrum that projects well into the somatic musculature:
    0: absent
    1: present

C h a r a c t e r 94. Rib and parapophysis of third centrum anteriorly elongate proximally, rib truncate distally, and a thin curved transformator process attached to gasbladder:
    0: absent
    1: present

C h a r a c t e r 95. The tripus fuses to the centrum by a thin, flexible lamellae as can be seen in early ontogeny in diplomystids, ictalurids, nematogenyids, trichomicterids, and other catfishes; however, as results of the growth of the surrounding bones and the movement of the tripus, the lamellae are commonly fragmented from early in ontogeny.

95) Parapophysis of tripus fused to the centrum (early in ontogeny) by a thin, flexible bony lamella which projects posterodorsally from the centrum:
    0: absent
    1: present

C h a r a c t e r 96. Transformator processes of the tripus separated posteriorly by the width of the complex centrum:
    0: absent
    1: present

C h a r a c t e r 97. Shortened pleural rib of the fourth centrum, and rib and parapophysis fused to each other, and having a median process, the os suspensorium, which is attached both to the mesentery suspending the gasbladder and gasbladder itself:
    0: absent
    1: present

C h a r a c t e r 98. 'Transverse process' of the fourth vertebra with an ovoid, anterolateral face which approaches the suspensorium of the pectoral fin:
    0: absent
    1: present

C h a r a c t e r 99. 'Transverse process' of the fourth vertebra expanded in a horizontal plane and the ovoid anterior face articulates with the suspensorium of the pectoral fin:
    0: absent
    1: present

C h a r a c t e r 100. 'Transverse process' of the fourth vertebra fused to the complex centrum:
    0: absent
    1: present

C h a r a c t e r 101. Os suspensorium with an elongate anterior horizontal process which is closely applied to surface of vertebral centra 2—4:
    0: absent
    1: present

C h a r a c t e r 102. Os suspensorium without posteromedial process:
    0: absent
    1: present

C h a r a c t e r 103. All pleural rib elements, particularly the fourth pleural rib and tripus, project from the centra at an angle close to the horizontal:
    0: absent
    1: present

C h a r a c t e r 104. Single ossified element that comprises supracleithrum, ossified Baudelot's ligament, and perhaps also the posttemporal:
    0: absent
    1: present

C h a r a c t e r 105. Reduction of number of postcleithra to one or none:
    0: absent
    1: present

C h a r a c t e r 106. Baudelot's ligament attached to the skull in the region of the cranial condyle or the lagenar capsula:

    0: absent

    1: present

C h a r a c t e r 107. Thick Baudelot's ligament bifurcated distally:

    0: absent

    1: present

C h a r a c t e r 108. Anterior and posterior parts of Baudelot's ligament attached to the cleithrum:

    0: absent

    1: present

C h a r a c t e r 109. More posterior pectoral fin-rays offset posteriorly from the anterior ray:

    0: absent

    1: present

C h a r a c t e r 110. Flanges for muscle attachment proximally on the ventral pectoral ray halves about equal in size to those on the dorsal pectoral ray halves:

    0: absent

    1: present

C h a r a c t e r 111. Pelvic girdle and fin:

    0: present

    1: absent

C h a r a c t e r 112. Dorsal fin:

    0: present

    1: absent

C h a r a c t e r 113. Anal fin elongate, extending along nearly the entire ventral margin of the body, from the region of the pectoral-fin origin anteriorly to the caudal fin or caudal filament posteriorly:

    0: absent

    1: present

C h a r a c t e r 114. Middle radial ossification along the entire length of both dorsal and anal fin pterygiophores:

    0: present

    1: absent

C h a r a c t e r 115. Anal fin-rays articulate directly with the proximal radials and distal radials are reduced:

    0: absent

    1: present

C h a r a c t e r 116. Principal caudal fin-ray count is 9/9 or less:

    0: absent

    1: present

C h a r a c t e r 117. Caudal support skeleton consolidated into a single element and caudal fin greatly reduced in size or absent:
>   0: absent
>   1: present

C h a r a c t e r 118. Haemal arches anterior to that of second preural centrum are laterally unfused in part of the outgroup (e.g., elopomorphs; Schultze & Arratia 1988), whereas they are laterally fused in other part of the outgroup (e.g., osteoglossomorphs, clupeomorphs, salmonids; Schultze & Arratia 1988, 1989, Arratia 1991, Arratia & Schultze in press). However, there are significant differences in the time that the fusion occurs between the perichondral ossification of the haemal arch and the autocentrum. I modify this character as follows:
>   118) Haemal arches anterior to that of second preural centrum perichondrally fused to the autocentrum from early ontogeny:
>   0: absent
>   1: present

C h a r a c t e r 119. According to Fink & Fink (1981), the haemal spine of preural centrum 1, the parhypural and hypural 1 are fused to the compound centrum at some stage of development. This is not completely correct because the parhypural and the hypural do not fuse to a 'compound centrum'. According to my studies on the development, histology, and macromorphology of the caudal skeleton I modify this character as follows:
>   119) Cartilaginous or ossified arcocentra of preural centrum 1 and that at the base of hypural 1 are fused to the 'compound centrum' in some stage of development:
>   0: absent
>   1: present

C h a r a c t e r 120. Hypural 1 separated from the 'compound centrum' by a hiatus in adult stage:
>   0: absent
>   1: present

C h a r a c t e r 121. Hypural 2 fused to a 'compound centrum':
>   0: absent
>   1: present

C h a r a c t e r 122. Epurals:
>   0: three
>   1: two or fewer

C h a r a c t e r 123. Dorsal and pectoral fin spines:
>   0: present
>   1: absent

C h a r a c t e r 124. A unique alarm substance is present in the epidermis of the skin in most ostariophysans. It is unknown if diplomystids produce the alarm substance. Gymnotoids lack the substance (Pfeiffer 1977).

124) Unique alarm substance in the epidermis:
    0: absent
    1: present

C h a r a c t e r 125. Ostariophysans have nuptial tubercles with a well developed keratinous cap (Wiley & Collette 1970). I have never seen nuptial tubercles with or without a keratinous cap in diplomystids. Keratinous skins are known in some siluroids (Wiley & Collette 1970, Arratia 1987a); apparently keratinous tubercles are not associated with breeding behaviour in siluroids.

125) Nuptial tubercles with a well developed keratinous cap:
    0: absent
    1: present

C h a r a c t e r 126. Electrogenic condition:
    0: absent
    1: present

C h a r a c t e r 127. Anus located well anterior on the body, ventral or anterior to the pectoral-fin origin:
    0: absent
    1: present

C h a r a c t e r 128. Scales on body:
    0: present
    1: absent

C h a r a c t e r 129. Adipose fin:
    0: absent
    1: present

C h a r a c t e r 130. Posteromedial extension of the perilymph system of the ear, sinus impar, communicates to the ear vibrations transmitted from the gasbladder by modified skeletal structures of the anterior vertebrae:
    0: absent
    1: present

First cladistic analysis

When the 37 characters of the suspensorium (1—37) presented above and in Appendix 1 are analyzed using the PAUP 3 program, only three trees are generated (consistency index = 0.956; tree length = 45). The consensus tree differs in the arrangement of the gonorynchiforms, cypriniforms, and characiforms from that of Fink & Fink (1981: Fig. 1) and in Otophysi not being monophyletic (compare Figs. 45A & 45B).

The scheme of relationships generated with the 37 characters from the suspensorium is represented in figure 45B. Node A corresponds to the trichotomy among Gonorynchiformes, [Cypriniformes + Characiformes], and [Siluroidei + Gymnotoidei]. Node B corresponds to the branching of cypriniforms and characiforms, and is supported by two synapomorphies. Among the studied ostariophysans, the suspensorium of characiforms is the most generalized; it is characterized by one homoplasy; cypriniforms share
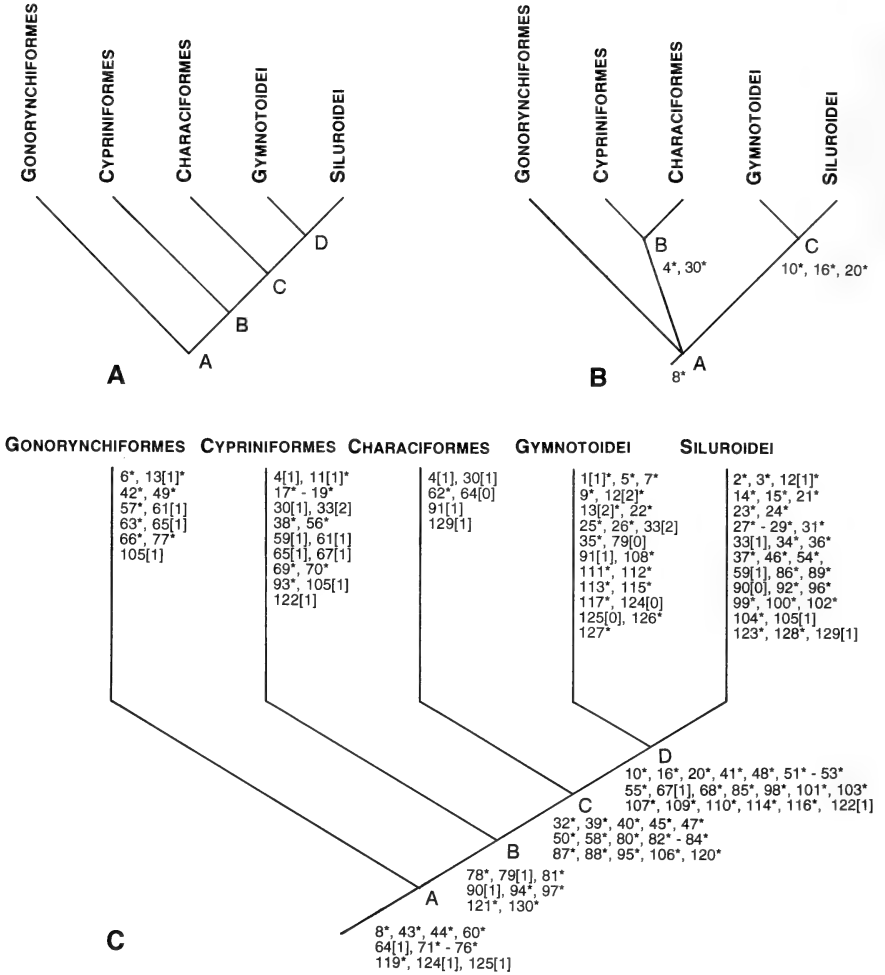
Fig.45: Hypothesis of phylogenetic relationships of ostariophysans. — A: According to Fink & Fink (1981); B: Based on 37 characters of the suspensorium (consistency index 0.956). Only the unique derived characters (*) are presented. For explanation of characters and character states see text and Appendix 1; C: Based on 130 morphological characters (consistency index 0.888). Homoplasies are presented by their character states, but an asterisk represents a unique derived character.

three unambiguous synapomorphies and one homoplasy. Node C corresponds to the branching of Siluroidei and Gymnotoidei and is supported by three synapomorphies.

The results of this study — based only on the suspensorium — partially support the schemes of relationships proposed by Rosen & Greenwood (1970), Roberts (1973), and Fink & Fink (1981) at the level of [Cypriniformes + Characiformes] and [Siluroidei + Gymnotoidei]. The sister-group relationship between catfishes and gymnotoids proposed by Fink & Fink (1981) is supported by additional characters of the suspensorium.

Second cladistic analysis

When the 37 characters of the suspensorium (1—37) plus 93 characters outside the suspensorium (from Fink & Fink 1981) presented above and in Appendix 1 are analysed using the PAUP 3 program, only one tree is generated (consistency index 0.888; tree length = 152). This tree has the same arrangement from that of Fink & Fink (1981) (compare Figs. 45A & 45C). There are no differences in the topology of the tree when the 130 characters are considered as ordered or unordered, but a slight difference in the consistency indices (0.888 and 0.871, respectively). There are no differences in the topology of the trees when all non-applicable conditions are coded as "2" (e.g., characters 1, 4, 11, 12, 12, and 13) or as "?", but a slight difference in the consistency indeces (0.888 and 0.885, respectively).

The suspensorium of ostariophysans provides a few synapomorphies at the higher levels. For example, one synapomorphy shared by ostariophysans (characters 8[1]): absence of a dermopalatine (see Fink & Fink 1981, Arratia & Schultze 1991). One synapomorphy (character 32[1]) shared by the characiphysans: hyomandibula articulates with the neurocranium through a single articular facet (Table 1). Three synapomorphies (characters 10[1], 16[1], and 20[1]) are shared by the siluriforms: anterior cartilage of autopalatine does not have contact with neurocranium; ligamentum primordiale inserts on the dorsal tip of the lower jaw; and ectopterygoid rudimentary or absent.

The suspensorium provides a few characters supporting the gonorynchiforms (characters 6[1] and 13[1]); the cypriniforms (characters 4[1], 11[1], 17[1], 18[1], 19[1], 30[1], and 33[1]); and the characiforms (characters 4[1] and 30[1]). In contrast, the suspensorium provides numerous synapomorphies for gymnotoids (characters 1[1], 5[1], 7[1], 9[1], 12[2], 13[2], 22[1], 25[1], 26[1], 33[2], and 35[1]), and siluroids (characters 2[1], 3[1], 12[1], 14[1], 15[1], 21[1], 23[1], 24[1], 27[1], 28[1], 29[1], 31[1], 33[1], 34[1], 36[1], and 37[1]). Character-states 1[2] and 4[2] are similar states to 3[1], therefore only the last one is counted as a siluroid synapomorphy. Character-states 11[2] and 13[2] are similar, therefore only 12[2] is counted as a gymnotoid synapomorphy.

Although I have modified several characters by Fink & Fink as shown above, eliminate a few of them from this analysis because of variation in the outgroup and/or ingroup, and added new ones, my results confirm the scheme of relationships of the ostariophysans published by Fink & Fink (1981: Fig. 1).

For characters supporting the different nodes see figure 45C, Appendix 1, and description of characters presented above.

RELATIONSHIPS AMONG PRIMITIVE CATFISHES

First cladistic analysis

The relationships among a few primitive catfishes are evaluated on the basis of the 75 characters listed below; the gymnotoids (first outgroup) and the characiforms (second outgroup) are considered as a combined outgroup, following the results by Fink & Fink (1981) and of the present study.

Diplomystids exhibit variability in some characters; all variable taxa present in Appendix 2 are considered in the analyses (Figs. 46A—C, 47A—E) as bearing only the derived states. For example, characters 16[1] and 44[1] in *Diplomystes camposensis*; characters 16[1] and 66[3] in *D. chilensis*; characters 16[1], 21[1], 24[1], 42[1], and 66[3] in *Olivaichthys viedmensis*. See Appendix 2 for the matrix of character states. Characters are explained below.

C h a r a c t e r 1. A dentate maxilla (Figs. 16A, 18B, 19B, 22A, C) is present in primitive catfishes including the Diplomystidae (e.g., Eigenmann 1927, Alexander 1965, Gosline 1975, Arratia 1987a), and †Hypsidoridae (Grande 1987). The presence of maxillary teeth has been interpreted as the primitive condition by most authors; however, McAllister (1968) considered it a secondarily derived condition. The presence of maxillary teeth in primitive catfishes may have different interpretations depending on the outgroups. Most ostariophysans do not have maxillary teeth, with the exception of the characiforms and primitive siluroids (i.e., Diplomystidae and †Hypsidoridae). The distribution of this character (Fig. 48) among extant ostariophysans, indicates that the presence of maxillary teeth has two possible interpretations: it may be a reversal from the condition present in primitive teleosts such as primitive clupeomorphs, osteoglossomorphs, and elopomorphs, or it may be a new formation because it is not present

Fig.46: Hypotheses of phylogenetic relationships of certain primitive catfishes based on 75 morphological characters. All characters are ordered with the exception of characters 1, 5, 7, 9, 47, 63, and 66. Characters are explained in the text; for character states see Appendix 2. Homoplasies are presented by their character states, but an asterisk represents a unique derived character. — A: Consensus tree of two equally parsimonious trees (consensus index 0.672); B—C: Topologies showing probable phylogenetic relationships among diplomystids.

Fig.47: Hypotheses of phylogenetic relationships of certain primitive catfishes based on 75 morphological characters. All characters are unordered. Characters are explained in the text; for character states see Appendix 1. Homoplasies are presented by their character states, but an asterisk represents a unique derived character. — A: Consensus tree of four equally parsimonious trees (consistency index 0.672); B—E: Topologies showing probable phylogenetic relationships among diplomystids.

in any of the possible ancestors of characiforms and siluriforms. By comparison with the combined outgroup and with most ostariophysans, I consider the absence of maxillary teeth as the primitive condition (see Appendix 2).

The absence of maxillary teeth is a synapomorphy of Siluroidea according to Grande (1987). However, I consider the presence of teeth along most of the oral margin as a synapomorphy of diplomystids, and the teeth anteriorly placed on the maxilla as an autapomorphy of †*Hypsidoris*.

Teeth along most of the oral margin of maxilla (Figs. 11, 19B) are present in parallel in *Hoplias* and diplomystids, however in *Xenocharax* there are only a few teeth in a single row close to the articular process of the maxilla. In †*Hypsidoris*, the teeth are also concentrated anteriorly, close to the articular process (Fig. 22C). Most catfishes do not have maxillary teeth; however, the presence of teeth placed anteriorly in the maxilla is an autapomorphy of †*Hypsidoris*.

   1) Maxilla with:
      0: no teeth
      1: teeth along most of the oral margin
      2: teeth anteriorly placed
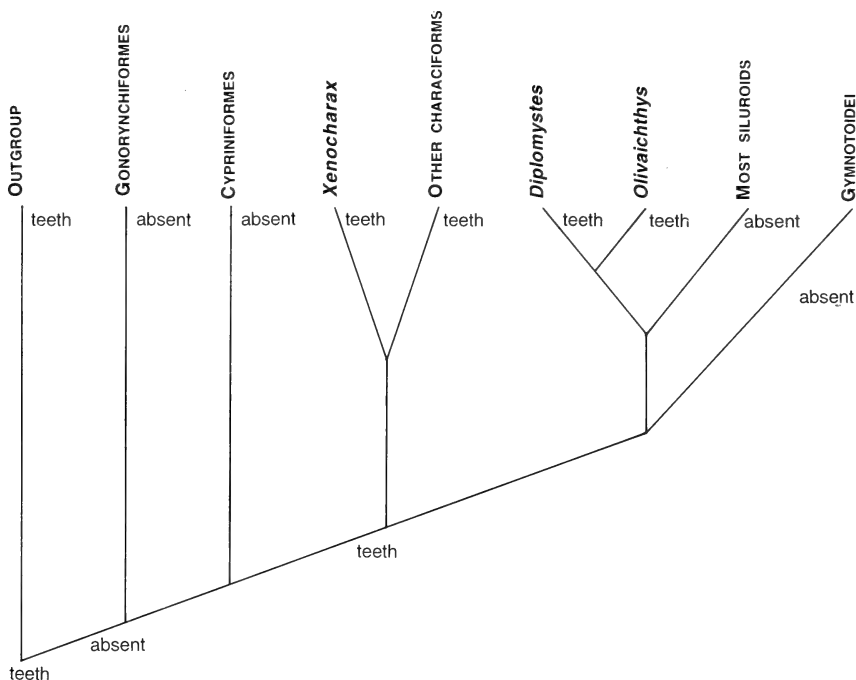
Fig.48: Distribution of maxillary teeth in ostariophysans (hypothesis of interrelationships after Fink & Fink 1981 and present paper).

C h a r a c t e r 2. A maxilla with several rows of teeth occurs in parallel in †*Hypsidoris* and the diplomystid *Olivaichthys*. The presence of one or two rows of teeth in the maxilla is the common condition found in *Diplomystes*.

    2) Maxilla:

        0: without teeth

        1: with one or two rows of teeth

        2: several rows of teeth

C h a r a c t e r 3 and 4. A single elongate anterior process of the maxilla bearing one articular facet for the pars autopalatina or the autopalatine is present in gymnotoids and characiforms respectively; in the Diplomystidae the process carries two facets for the articulation with the autopalatine. These facets are parallel to each other and they may be close to each other as in *Diplomystes camposensis* (Fig. 19A) or they may be broadly separate as in *D. nahuelbutaensis* (Fig. 18B). The facets may be seen as slight concavities (e.g., *D. camposensis*), or as short, broad projecting processes (e.g., *D. nahuelbutaensis*). In most siluroids, the anterior articular region of the maxilla is rudimentary and modified into two rudimentary processes, each of which articulate with the autopalatine. This feature is a synapomorphy of †*Hypsidoris* plus Siluroidea (=Siluroidei sensu Grande 1987).

3) Maxilla that has two small articular facets for the autopalatine, both on two rudimentary processes:

0: absent

1: present

4) Maxilla that has two large articular facets for autopalatine broadly separated from each other, both on two rudimentary processes at the elongate anterior maxillary process (Fig. 18B):

0: absent

1: present

This feature is an autapomorphy of *Diplomystes nahuelbutaensis*; this new character should be added to the diagnosis given by Arratia (1987a).

C h a r a c t e r 5. The most common condition in siluriforms is the presence of two autopalatal processes on the maxilla that articulate with the anterior cartilage of the autopalatine. These two autopalatal processes are well developed in †*Hypsidoris*; but they are small in most catfishes. In the Diplomystidae, there is only one maxillary anterior process, but with two articulations, that separates the premaxilla and autopalatine (Fig. 19A—C); however, in young diplomystids the anterior cartilage of the autopalatine touches the premaxilla. The condition present in adult Diplomystidae is unique among the siluriforms. In †*Hypsidoris*, the two well-developed autopalatal processes extend between the autopalatine and premaxilla; probably the processes separated both bones completely.

The loss of the single elongate anterior process of the maxilla was considered a synapomorphy of the Siluroidea by Grande (1987: character 6); this character is confirmed herein. The presence of two well-developed anterior processes (character 5[1]) is an autapomorphy of †*Hypsidoris*.

5) Maxilla:

0: with one long anterior process separating the autopalatine (when present) from the premaxilla or with slight contact betwen the autopalatine and premaxilla

1: with two well-developed anterior processes that separate the autopalatine and premaxilla

2: without the long anterior process

C h a r a c t e r 6. The maxilla of most catfishes is small, therefore the enlarged premaxillae form most of the upper oral margin. The size and shape of the maxilla differs among catfishes; it is longest and most distally expanded in diplomystids (Figs. 19A, 20A—C). In †*Hypsidoris* it is comparatively shorter than in diplomystids and slightly expanded distally (Fig. 22A, C). In most siluroids it is reduced to just the anterior portion. The loss or reduction of the distal portion of the maxilla is a synapomorphy of the Siluroidea according to Grande (1987: character 5); this character is confirmed herein.

6) Maxilla:

0: with elongate or slightly elongate body expanded distally

1: rudimentary

C h a r a c t e r 7. The autopalatine of characiforms is shorter than that of catfishes; it largely corresponds to the anterior part of the catfish autopalatine (Fig. 6C—D). A rod-like autopalatine (Figs. 26A, B, 27A—D, 32, 34A, B, 35A, C) is the common condition for catfishes; however, an autopalatine that is broad anteriorly, and elongate and narrow posteriorly, is true of a few catfishes such as the diplomystids, †hypsidorids, and nematogenyids (Figs. 18A, 22D, 28D). In trichomycterines, the autopalatine is broad anteriorly but the posterior part becomes narrower gradually, therefore the posterior part is not as elongate and slender as in diplomystids (Arratia 1990a).

The presence of a extremely small or rod-shaped autopalatine is a synapomorphy of the Siluroidea according to Grande (1987); however, the Nematogenyidae and Trichomycteridae have well-developed autopalatines, expanded anteriorly (Figs. 28D, 29A, B; Arratia 1987a, 1990a, Arratia & Menu Marque 1984). The presence of a rod-shaped autopalatine is a synapomorphy of the Ictaluridae and most advanced catfishes (Fig. 46A). The presence of an autopalatine that is broad anteriorly, and elongate posteriorly, is a synapomorphy of the primitive catfishes (= Siluroidei sensu Fink & Fink 1981; Siluriformes sensu Grande 1987).

    7) Autopalatine, when present:
        0: short, slightly broad anteriorly
        1: broad anteriorly, narrow and elongate posteriorly
        2: rod-like

C h a r a c t e r 8. The autopalatine abutting a cavity on the dorsal aspect of the premaxilla is the common condition in characiforms and most catfishes (Figs. 29A, B, 33, 34B, 36A). In diplomystids, however, the autopalatine does not abut the dorsal surface of the premaxilla and this is therefore a synapomorphy of the Diplomystidae. The anterior cartilage of the autopalatine is not preserved in the material available of †*Hypsidoris*. Due to the breadth and size of the anterior part of the autopalatine in †*Hypsidoris* (Fig. 22B), I suspect that the situation was similar to that in the Diplomystidae. However, I prefer to code this character as unknown (?) (see Appendix 2). In most catfishes, the anterior cartilage or fibrocartilage of the autopalatine retains its position with respect to the dorsal aspect of the premaxilla through the action of connective tissue and ligaments. In trichomycterines however, a synchondral articulation is formed during growth between the anteromedial portion of the cartilage of the autopalatine and the premaxilla.

    8) Autopalatine, when present, that abuts the dorsal surface of the premaxilla:
        0: present
        1: absent

C h a r a c t e r 9. In most teleosts the maxilla and autopalatine are joined by a single articulation; however, a double, anteroventral articulation is a synapomorphy of the catfishes. The double articulation is anteroventrally oriented in diplomystids and †hypsidorids (my interpretation of Grande's 1987 figures) but is lateroventrally oriented in other catfishes. The presence of a double anteroventral articulation is therefore a synapomorphy of the Siluroidei sensu Fink & Fink (1981) = Siluriformes sensu Grande (1987), and the presence of a lateroventral articulation between the autopalatine and maxilla is a synapomorphy of the Siluroidea.

9) Articulation between autopalatine, when present, and maxilla that is:
    0: single, laterally oriented
    1: double, anteroventrally oriented
    2: double, lateroventrally oriented

C h a r a c t e r 10. A hinge joint between the autopalatine and maxilla is the common condition among characiforms and catfishes; the presence of this joint permits an enormous mobility of the maxilla and autopalatine in both young and juvenile individuals. With increased growth, the autopalatine loses this mobility (e.g., *Nematogenys, Parapimelodus*). In diplomystids, the anterior process of the maxilla articulates via two articular facets in the same plane as the autopalatine; however, the maxilla is not displaced along the body axis as in other catfishes.

    10) Hinge joint between the maxilla and autopalatine, when present:
        0: absent
        1: present

C h a r a c t e r 11. The absence of the autopalatine extension dorsal to the dermal entopterygoid is a synapomorphy of the Siluroidea. The condition is variable in *Diplomystes* because many specimens lack the entopterygoid.

    11) Posterior part of the autopalatine, when present, extending dorsally to reach the dermal entopterygoid:
        0: present
        1: absent

C h a r a c t e r 12. The presence of the posterior cartilage of the autopalatine, 'entopterygoid', and metapterygoid (Fig. 28D) in the same plane is an autapomorphy of the Nematogenyidae (Arratia 1990a).

    12) Posterior cartilage of the autopalatine, when present, 'entopterygoid', and metapterygoid in the same plane:
        0: absent
        1: present

C h a r a c t e r 13. The presence of the posterior part of the autopalatine extension dorsal to the metapterygoid alone, is a homoplastic feature that characterizes trichomycterines (Arratia & Menu Marque 1984, Arratia 1990a), *Heptapterus*, and *Parapimelodus* (Fig. 34B) among the studied catfishes.

    13) Posterior part of autopalatine, when present, extends dorsally to reach only the metapterygoid:
        0: absent
        1: present

C h a r a c t e r 14. The posterior part of the autopalatine is dorsal or dorsolateral to the 'entopterygoid' alone in *Ameiurus, Ictalurus*, and *Pylodictis* (Fig. 27A—D) among the studied catfishes.

    14) Posterior part of autopalatine dorsal or dorsolateral to only the 'entopterygoid':
        0: absent
        1: present

C h a r a c t e r 15. A large cartilage is present between the mesethmoid, vomer, lateral ethmoid, and orbitosphenoid in diplomystids. A bony contact between the autopalatine and vomer is therefore missing and these bones articulate with each other through this cartilage. In more advanced catfishes the area of cartilage is small and lies between only the mesethmoid, vomer, and lateral ethmoid (e.g., *Nematogenys*) so that the auto-palatine and vomer articulate directly. An articulation between the autopalatine and vomer is entirely missing in other catfishes (e.g., *Ictalurus*). I would predict that a direct articulation between the autopalatine and vomer is a synapomorphy of the Siluroidei. The absence of an articulation between the autopalatine and vomer is a homoplastic feature characteristic of ictalurids, *Heptapterus, Rhamdia*, and *Parapimelodus*.

15) Pars autopalatina or autopalatine articulates with vomer:
    0: through cartilage
    1: directly
    2: no articulation is present between these bones

C h a r a c t e r 16. The absence of a subautopalatine tooth plate is the widespread con-dition in the outgroup; however, *Hoplias* — among the studied characiforms — bears a subautopalatine toothplate. The presence of a subautopalatine toothplate is con-sidered herein to be independently derived in *Hoplias* (Fig. 11), *Diplomystes chilensis, Olivaichthys* (Fig. 19D), and †*Hypsidoris* (Fig. 22C).

16) Subautopalatine toothplate that attaches to the autopalatine:
    0: absent
    1: present

C h a r a c t e r 17. The absence of a dermal ectopterygoid is hypothesized here as a synapomorphy of the Siluroidea. The condition is variable in *Diplomystes* because many specimens lack an ectopterygoid.

17) Dermal ectopterygoid that is present ventral or partially ventral to the autopalatine:
    0: present
    1: absent

C h a r a c t e r 18. The presence of a sesamoid ectopterygoid joining the autopalatine and 'entopterygoid' is a synapomorphy of a clade including *Parapimelodus, Bagre*, and *Galeichthys*.

18) Sesamoid ectopterygoid that joins the autopalatine and 'entopterygoid':
    0: absent
    1: present

C h a r a c t e r 19. The absence of a dermal entopterygoid is hypothesized here to be a synapomorphy of the Siluroidea. The small entopterygoid is absent in some diplo-mystids.

19) Dermal entopterygoid:
    0: present
    1: absent

C h a r a c t e r 20. The attachment by ligaments and/or connective tissue between the 'entopterygoid' and the lateral ethmoid is a derived condition of catfishes above the

level of [*Nematogenys* + *Trichomycterus*] in figure 46A. This character is coded with a question mark for *Trichomycterus* because this taxon lacks the 'entopterygoid'.

The presence of a ligament and/or connective tissue extending between the entopterygoid and the lateral ethmoid is a homoplastic character that occurs above the level of the ictalurids (Fig. 46A) and occasionally in *Olivaichthys*. A reversal is found in *Parapimelodus*.

20) A ligament and/or connective tissue attaches the 'entopterygoid' to the lateral ethmoid:
    0: absent
    1: present

C h a r a c t e r 21. The presence of a link between the 'entopterygoid' and vomer is predicted as a synapomorphy of the Siluroidea.

21) A ligament and/or connective tissue attaches the 'entopterygoid' and the vomer:
    0: absent
    1: present

This is a homoplastic character that is not found in *Trichomycterus* (without 'entopterygoid') and that has a reversal in *Parapimelodus*.

C h a r a c t e r 22. A short ligamentous connection between the autopalatine and metapterygoid is present in catfishes, including diplomystids, nematogenyids, and trichomycterines. In *Ictalurus, Pylodictis*, and *Noturus*, a short, dense link of connective tissue is present. The presence of a link between these bones is a synapomorphy of the catfishes; however, this feature is lost in more advanced catfishes. A link between these bones is absent in the 'pimelodids' such as *Heptapterus, Rhamdia, Cetopsorhamdia, Pimelodella, Pimelodus*, and *Parapimelodus*, and also in *Galeichthys* and *Bagre marinus*; this secondary loss or reversal characterizes catfishes more advanced than ictalurids in figure 46A.

22) Autopalatine and metapterygoid that are linked by a ligament or connective tissue:
    0: absent
    1: present

C h a r a c t e r 23. The metapterygoid-vomer ligament arises in parallel in Diplomystidae, *Trichomycterus*, and [*Bagre* + *Galeichthys*] (Fig. 46A).

23) Metapterygoid-vomer ligament:
    0: absent
    1: present

C h a r a c t e r 24. The presence of a metapterygoid-'entopterygoid' ligament characterizes the clade that includes ictalurids and more advanced catfishes (Fig. 46A). A ligament also occurs in *Nematogenys* and in a few individuals of *Olivaichthys*. It is most parsimonious to interpret the 'entopterygoid' and its ligament present in *Olivaichthys* as a new formation, because the 'entopterygoid' type 1 in *Olivaichthys* is present together with a dermal entopterygoid. Therefore, it is not possible to consider this bone homologous with a dermal entopterygoid or 'entopterygoid' present in advanced catfishes.

24) Metapterygoid-'entopterygoid' ligament:

    0: absent

    1: present

C h a r a c t e r 25. The common condition among catfishes is the presence of a metapterygoid and hyomandibula that are sutured to each other. The metapterygoid and hyomandibula do not articulate with each other in *Heptapterus, Rhamdia*, and *Parapimelodus* as well as in certain 'bagrids'; this character that appears to be a 'pimelodid' synapomorphy is, in the context of all the other data, interpreted by the PAUP analysis as a derived condition of [*Heptapterus* + [*Rhamdia* + [*Parapimelodus* + [*Bagre* + *Galeichthys*]]]] (Fig. 46A). Note, however, that the last two genera are characterized by the presence of a suture between the metapterygoid and hyomandibula.

25) Metapterygoid and hyomandibula:

    0: synchondrally articulating and/or sutured to each other

    1: separate from each other (no articulation present)

C h a r a c t e r 26. The presence of a notch separating the processus basalis and the posterodorsal part of the metapterygoid is the primitive condition in teleosts (Arratia & Schultze 1991). The loss of this notch is a synapomorphy of the Siluroidea (homoplastic character).

26) Metapterygoid with a notch separating the processus basalis from the posterodorsal part of the bone:

    0: present

    1: absent

C h a r a c t e r 27. Dermo + metapterygoid:

    0: absent

    1: present

C h a r a c t e r 28. The presence of a well-developed anteroventral process of the metapterygoid, the ectopterygoid process (Figs. 16A—C, 17A, 28D), is a homoplastic character present at least in diplomystids, nematogenyids, and the clade including [*Parapimelodus* + [*Bagre* + *Galeichthys*]]. It is not, however, present in all; for example, the ectopterygoid process is absent in ictalurids and trichomycterids.

28) Ectopterygoid process of metapterygoid:

    0: absent

    1: present

C h a r a c t e r 29. A well-developed lateral process of the metapterygoid is present in ictalurids such as *Pylodictis* and a few species of *Ictalurus* (Fig. 40B—D). The presence of this process is a unique derived condition. In addition, there is another character associated with the presence of this process: the anterior development of the levator arcus palatini muscle that inserts on the lateral process of the metapterygoid (unlike any other catfish studied here).

29) Well-developed lateral process on the lateral surface of the metapterygoid for insertion of the levator arcus palatini muscle:

    0: absent

    1: present

C h a r a c t e r 30. The presence of a bone-to-bone articulation between the hyoman-
dibula and pterosphenoid is an autapomorphy of the Diplomystidae. This articulation
develops throughout ontogeny in diplomystids. The hyomandibula that articulates with
autosphenotic only is a synapomorphy of the clade that includes ictalurids plus more
advanced catfishes (Fig. 46A).

    30) Hyomandibula that articulates with autosphenotic and pterotic only:
        0: absent
        1: present

C h a r a c t e r 31. A levator arcus palatini crest is present on the lateral surface of the
hyomandibula for the attachment of the levator arcus palatini muscle. In diplomystids
(Fig. 21A—D) — except *Diplomystes camposensis* (Figs. 16B, C, 17A) — and *Ictalurus*
(Fig. 26C) the crest is well-developed and mainly horizontal to the dorsal margin of the
hyomandibula. In other catfishes the crest may be vertically placed and is not well-
developed (e.g., *Nematogenys*; Fig. 28C). There are however some exceptions such as
Clarias.

The presence of a well-developed horizontal levator arcus palatini crest is a derived
feature of *Diplomystes nahuelbutaensis, D. chilensis, Olivaichthys,* and *Ictalurus*. In
contrast, Bornbusch (1991) interpreted the presence of a prominent crest as the
primitive state for Siluroidea. The difference in our interpretations of this character is
based on his interpretation of the presence of a prominent crest in †*Hypsidoris* (in my
opinion, it is not well-developed as in certain diplomystids and ictalurids; PU 20570 a;
Fig. 23).

    31) Horizontal levator arcus palatini crest on the lateral surface of the hyoman-
    dibula:
        0: rudimentary or absent
        1: well developed

C h a r a c t e r 32. The hyoideomandibularis nerve trunk runs in a canal inside the
bone in ostariophysans excluding diplomystids, where the nerve runs on the lateral
aspect of the hyomandibula (Fig. 21A, B; Arratia 1987a). The lateral course of the
hyoideomandibularis nerve trunk is an autapomorphy of the Diplomystidae.

    32) Hyoideomandibularis nerve trunk lateral to the hyomandibula:
        0: absent
        1: present

C h a r a c t e r 33. A small elongate bone (Fig. 49) uniting epibranchial 1 and the
hyomandibula is absent in primitive characiforms and gymnotids as well as in most cat-
fishes; however, this element is present in diplomystids and a few other catfishes (e.g.,
Rhamdia). The small bone present in diplomystids was identified as pharyngobranchial
1 by Arratia (1987a: Fig. 27C); however, this bone has a unique location and relation-
ships unlike pharyngobranchial 1 of other primitive teleosts. The presence of pharyn-
gobranchial 1 however, must be considered homoplastic because it is present in
Diplomystidae and also in the clade formed by [*Rhamdia* + [*Parapimelodus* + [*Bagre*
+ *Galeichthys*]]] (Fig. 46A).
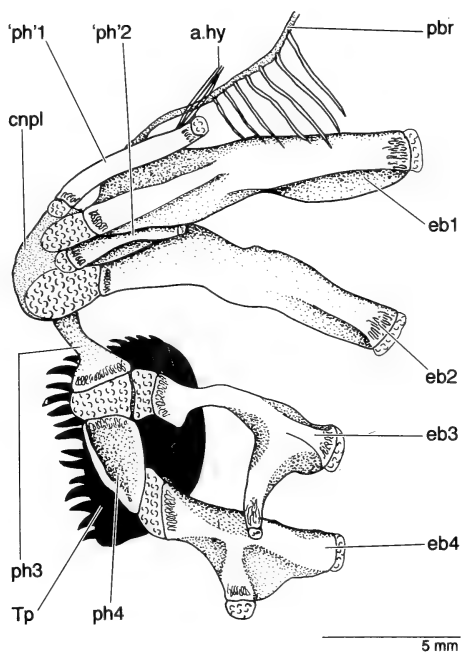
Fig.49: Upper section and branchial arches of *Diplomystes camposensis*, right side, dorsal view (PC 110276).
a.hy: attachment to hyomandibula; cnpl: plate of connective tissue; eb 1-4: epibranchial 1-4; ph 1-2: pharyngobranchial 1-2; ph 3-4: pharyngobranchial 3-4; pbr: pseudobranch; Tp: toothplate.

33) Small, elongate pharyngobranchial that is attached to epibranchial 1 and the medial aspect of hyomandibula:

    0: absent

    1: present

C h a r a c t e r 34. A small pseudobranch (Fig. 49) is present in primitive catfishes such as diplomystids (Arratia 1987a) and nematogenyids. It is absent in most catfishes, as well as *Xenocharax* and *Hoplias* and gymnotoids. The pseudobranch is long in diplomystids and has a variable number of lamellae (9—15), whereas it is short in Nematogenyidae with 2 or 3 lamellae.

34) Pseudobranch that is imbedded in connective tissue to the medial aspect of the hyomandibula:

    0: absent

    1: present

C h a r a c t e r 35. The hyomandibular fossa is commonly formed by the sphenotic and pterotic; however, the prootic may also form part of the fossa (Table 1). The absence of the prootic in the hyomandibular fossa is a synapomorphy of catfishes above the level of [*Nematogenys* + *Trichomycterus*] (Fig. 46A).

35) Prootic participating in the framing of the hyomandibular fossa:

    0: present

    1: absent

C h a r a c t e r 36. The metapterygoid functioning as the main support of the eye is a synapomorphy of the primitive catfishes; however, this character has undergone several evolutionary transformations among siluroids (Arratia 1990a).

36) Metapterygoid functioning as the main support of the eye:
    0: absent
    1: present

C h a r a c t e r 37. The quadrate partially supporting the eye is unusual in teleosts; however, this condition is present in some catfishes such as *Heptapterus, Rhamdia, Parapimelodus*, and *Bagre*.

37) Quadrate functioning as one of the elements supporting the eye:
    0: absent
    1: present

Characters 38 to 41 are from Grande (1987); they were proposed as synapomorphies of the Siluroidei sensu Grande (38 to 40 herein) and of †Hypsidoroidea (41 herein).

C h a r a c t e r 38. The character proposed by Grande (1987) as a synapomorphy of the Siluroidei is "17 or fewer principal caudal rays (vs. 18 or more in *Diplomystes* and other primitive teleosts)." Most primitive extant teleosts have 19 principal caudal rays (Schultze & Arratia 1989), this however was not coded in this analysis because it is found outside of this taxonomic problem. The presence of 18 rays is an independently derived character of a few primitive extant teleosts such as the clupeomorph *Denticeps*, and of the siluriforms Diplomystidae and certain gymnotoids. Nematogenyidae are unique in that the procurrent rays become segmented during growth and all caudal rays are segmented in large adult individuals (Arratia 1982, 1983). An increase in the segmentation also has been observed in *Noturus* species (Schultze & Arratia 1989).

The presence of 17 caudal rays is a synapomorphy at the primitive level of Siluroidei (sensu Grande 1987); reduction in the number of principal caudal rays characterizes a number of different clades among the siluroids (Lundberg & Baskin 1969, Arratia 1982, 1983).

38) Caudal fin with:
    0: 18 or more principal caudal rays
    1: 17 or fewer principal caudal rays

C h a r a c t e r 39. A membranous bony extension on the ventral surface of the fifth centrum is absent in catfishes such as diplomystids, nematogenyids, and trichomycterids (Arratia 1987: Fig. 28A, Arratia & Menu Marque 1984: Fig. 3B). The presence of this membranous bony extension was considered as a synapomorphy of the Siluroidei by Grande (1987: character 2); however, it is interpreted herein as a homoplastic feature occurring in parallel in †*Hypsidoris* and the clade above the [*Nematogenys + Trichomycterus*] (Fig. 46A).

39) Membranous bony extension over the ventral surface of the fifth centrum:
    0: absent
    1: present

C h a r a c t e r 40. The fifth centrum closely joined to the complex centrum is a synapomorphy of the †*Hypsidoris* + Siluroidea according to Grande (1987: character 3). I am uncertain of the meaning of "joined closely" as stated by Grande (1987), because centra 4 and 5 become ankylosed or fused during growth in extant catfishes, except the Diplomystidae and *Trogoglanis* (Lundberg 1982); I have therefore modified this character to read "ankylosed or fused."

    40) Fifth centrum that is ankylosed or fused to the complex centrum:
        0: absent
        1: present

C h a r a c t e r 41. This character was proposed as the sole autapomorphy of the †Hypsidoroidea by Grande (1987); however, a well-developed coronoid process of the dentary (and also the angular) is present in trichomycterines (e.g., *Trichomycterus roigi*; Arratia & Menu Marque 1984: Fig. 7A—D). The presence of this character in both groups is interpreted here as independently derived.

    41) Unusually high and narrow coronoid process of the dentary and angular:
        0: absent
        1: present

Characters 42 to 68 are from Arratia (1987a).

C h a r a c t e r 42. In most catfishes the autosphenotic is smaller than or of similar length to the pterotic; however, an autosphenotic larger than the pterotic is present in catfishes such as diplomystids, except for a few individuals of *Olivaichthys* (Arratia 1987a: Figs. 4A, 13, 22A), and ictalurids (Lundberg 1982: Figs. 8A, 11A, B, 12A, B).

    42) Sphenotic of similar length to or smaller than pterotic:
        0: present
        1: absent

C h a r a c t e r 43. An extrascapular (Arratia 1987a: Figs. 4A, 13, 22A, 41A—C) is present in primitive catfishes; it is absent in catfishes such as loricarioids (e.g., Nematogenyidae, Trichomycteridae, and Loricariidae) and *Clarias*.

    43) Extrascapular:
        0: present
        1: absent

C h a r a c t e r 44. A suture between the pterosphenoid and parasphenoid is a synapomorphy of ictalurids and more advanced catfishes as shown in figure 46A. In juvenile *Bagre marinus* these bones almost contact each other; however, I am uncertain whether there is a suture between them in larger specimens. This character is variable in *Diplomystes camposensis*; only some specimens have the suture between the pterosphenoid and parasphenoid (Arratia 1987a: Fig. 23A).

    44) Suture between the pterosphenoid and parasphenoid:
        0: absent
        1: present

C h a r a c t e r 45. The presence of a long posterior part of the autopalatine, more than the half of the length of the bone (Figs. 17A, B, 18A) is a synapomorphy of *Diplo-*

mystes that it is lost in *Diplomystes chilensis* which has a very short autopalatine posteriorly (Fig. 17C).

 45) Posterior portion of the autopalatine that is long, more than half of the length of the bone:
  0: absent
  1: present

C h a r a c t e r 46. The most common condition in teleosts is the presence of an undivided autopalatine anteriorly (Figs. 4D, 6A—C). An anteriorly bifurcate autopalatine (Figs. 6D, 16A—C, 17A, B, 18A) is a synapomorphy of the Diplomystidae. The anterior fusion of both maxillary processes of the autopalatine (Fig. 17C) later in the ontogeny of certain individuals of *Diplomystes chilensis* and *Olivaichthys viedmensis* is a synapomorphy shared by these species.

 46) Anterior part of autopalatine:
  0: undivided
  1: divided into two elongate processes which remain separate in adults
  2: divided into two elongate processes which fuse anteriorly later in ontogeny

C h a r a c t e r 47. The presence of a coronomeckelian is common in teleosts; however, the coronomeckelian is absent in *Trichomycterus* as well as in other advanced loricarioids. The presence of a coronomeckelian bone that increases its size considerably during ontogeny is an autapomorphy of the Diplomystidae (Fig. 20B; Arratia 1987a).

 47) Coronomeckelian:
  0: small, enlarging moderately during ontogeny
  1: large, enlarging greatly during ontogeny
  2: absent

C h a r a c t e r 48. Dorsal and ventral hypohyals are about equal in size and shape in diplomystids (Arratia 1987a: Fig. 27B; Arratia & Schultze 1990: Fig. 4A). In most catfishes however, the ventral hypohyal is larger than the dorsal one (Arratia & Schultze 1990: Figs. 4B—D, 8A). The dorsal hypohyal is absent in catfishes such as trichomycterids and loricariids (Arratia & Menu Marque 1984: Fig. 8A; Arratia & Schultze 1990: Figs. 5A, 6A). The presence of both dorsal and ventral hypohyals of different sizes is hypothesized herein as a synapomorphy of †*Hypsidoris* + Siluroidea.

 48) Dorsal and ventral hypohyals:
  0: similar in size
  1: unequal in size
  2: dorsal hypohyals absent

C h a r a c t e r 49. The prootic and autosphenotic are fused in adult *Nematogenys* and *Trichomycterus*. In *Trichomycterus*, however, the pterosphenoid is also included in this fusion. The fusion of bones occurs early in ontogeny in trichomycterids, whereas fusion occurs during later growth in *Nematogenys*.

 49) Prootic and autosphenotic fusion:
  0: absent
  1: present

C h a r a c t e r 50. Vomer: A T-shaped or arrow-shaped bone is the generalized condition present in catfishes and this fact was established by Howes (1983b). The presence of an almost rhomboid vomer is an autapomorphy of the Diplomystidae (Arratia 1987a: Figs. 5A, 23A).

50) T-shaped or arrow-shaped anterior portion of the vomer:
    0: present
    1: absent

C h a r a c t e r 51. A separate first abdominal centrum is not unique for diplomystids among catfishes; a well-separated centrum also is present in †*Hypsidoris* (Grande 1987) and in some adult catfishes such as *Heptapterus, Rhamdia*, and *Parapimelodus.* Although this is a homoplastic character, the absence of a separate first centrum (due to loss or fusion) can be considered a synapomorphy of [*Nematogenys + Trichomycterus*] and of [*Bagre + Galeichthys*].

51) First centrum of the Weberian complex that is present as a separate element:
    0: present
    1: absent

C h a r a c t e r 52. The presence of a complex Weberian centrum formed by the fusion of centra 2—4 is a synapomorphy of the catfishes. The fusion of abdominal centra 2—5 is a synapomorphy of †*Hypsidoris* plus primitive members of Siluroidea. The addition of more posterior centra is a synapomorphy of [*Rhamdia* + [*Parapimelodus* + [*Bagre + Galeichthys*]]] (Fig. 46A).

52) Weberian apparatus includes:
    0: no fusion of centra
    1: fusion of abdominal centra 2—4
    2: fusion of abdominal centra 2—5
    3: fusion of abdominal centra 2—6 or more

C h a r a c t e r 53. The presence of a swimbladder divided into a pair of lateral vesicles is a synapomorphy of [*Nematogenys + Trichomycterus*] (Fig. 46A). This is not a unique condition because a swimbladder separated into two vesicles is also present in some other catfishes (Chardon 1968).

53) Swimbladder that is divided into a pair of completely separated lateral vesicles:
    0: absent
    1: present

C h a r a c t e r 54. Bony capsules around the swimbladder vesicles that only open laterally is a synapomorphy of [*Nematogenys + Trichomycterus*] (Fig. 46A), but not unique to these forms. Encapsulated swimbladder vesicles are also present in other catfishes such as loricariids, astroblepids, and perhaps callichthyids. However, it has not yet been demonstrated that the bony capsules are formed in the same way in all of these fishes.

54) Parapophyses of vertebrae 3—4 or 3—5 that form a bony capsule around the swimbladder vesicles that open only laterally:
    0: absent
    1: present

C h a r a c t e r 55. The presence of blood vessels running in a groove surrounded by lamellar walls in the ventral part of the Weberian apparatus occurs in parallel in †*Hypsidoris* and the clade including ictalurids plus more advanced catfishes (Fig. 46A). Blood vessels running in a tube-like lamellar formation ventral to the Weberian apparatus is a synapomorphy of [*Rhamdia* + [*Parapimelodus* + [*Bagre* + *Galeichthys*]]] (Fig. 46A).

   55) Blood vessels:
       0: ventral to the centra of the Weberian apparatus
       1: in a groove partially surrounded by lamellar walls in the ventral part of the Weberian apparatus
       2: enclosed in a tube-like lamellar formation ventral to the Weberian apparatus

C h a r a c t e r 56. The presence of four proximal pectoral radials is the primitive condition for teleosts; in contrast, three proximal pectoral radials are present in diplomystids (Arratia 1987a: Figs. 30A, D) and most other catfishes. When three proximal radials are present, the first radial is a large mass of cartilage that may ossify late in ontogeny, in addition to the two other elongate radials (Arratia 1987a: Fig. 30A). Three fully ossified, elongate proximal radials are present in *Nematogenys*. Two ossified radials or one ossified and one cartilaginous radial are present in trichomycterines. The presence of three proximal pectoral radials is a synapomorphy of primitive catfishes. The presence of three elongate well-ossified radials is an autapomorphy of the Nematogenyidae.

   56) Pectoral fin with:
       0: four proximal pectoral radials
       1: three proximal pectoral radials
       2: two or fewer proximal radials

C h a r a c t e r 57. Characiforms such as *Xenocharax* and *Hoplias* have a higher number of pelvic fin-rays (10 and 8, respectively) than most catfishes. Exceptions include *Ictalurus* (8) and *Pylodictis* (9). The presence of six pelvic fin-rays is a synapomorphy of catfishes. The high number of rays found in *Ictalurus* and *Pylodictis* is a secondarily derived condition.

   57) Pelvic fin, when present, with:
       0: more than six rays
       1: six rays
       2: less than six rays

C h a r a c t e r 58. Cartilaginous pelvic radials are usually absent in catfishes; however, a small cartilaginous pelvic radial has been observed in *Olivaichthys viedmensis* (Arratia 1987a: Fig. 37A) and *Noturus exilis*. The absence of a cartilaginous pelvic radial is a synapomorphy of catfishes. The presence of a cartilaginous pelvic radial in early ontogeny of *Olivaichthys viedmensis* is a reversal to the primitive condition, and therefore an autapomorphy of this species.

   58) Pelvic fin with cartilaginous radial:
       0: present
       1: absent

C h a r a c t e r 59. The presence of spines in the dorsal fin is a synapomorphy of catfishes. However, some catfishes lack spines (e.g., *Nematogenys* and *Trichomycterus*).

 59) Dorsal fin spines:

  0: absent

  1: present

C h a r a c t e r 60. A caudal fin with less than six hypurals occurs in parallel in [*Nematogenys* + *Trichomycterus*] and in the clade above the ictalurids in figure 46A.

 60) Caudal fin skeleton with six or more hypurals:

  0: present

  1: absent

C h a r a c t e r 61. The fusion of hypurals 1 and 2 is a homoplastic character occurring in [*Nematogenys* + *Trichomycterus*], *Heptapterus*, and [*Parapimelodus* + [*Bagre* + *Galeichthys*]].

 61) Hypurals 1 and 2:

  0: not fused to each other

  1: fused to each other

C h a r a c t e r 62. Hypural 1 fused to the parhypural represents the derived condition of *Trichomycterus*, but is not unique to trichomycterines (Lundberg & Baskin 1969).

 62) Hypural 1:

  0: not fused to the parhypural

  1: fused to the parhypural

C h a r a c t e r 63. The PAUP program interprets the presence of three or four pairs of barbels as a synapomorphy of the Siluroidea (however, it could be a synapomorphy of *Hypsidoris* [unknown condition] + Siluroidea) and the presence of one pair of barbels as an autapomorphy of Diplomystidae. The same result was obtained when the character was unordered.

 63) Barbels:

  0: absent

  1: present as only maxillary barbel

  2: present as more than one pair of barbels

C h a r a c t e r 64. The sensory canals in teleosts may be simple, branched, or reduced (Webb 1989). These three conditions are present in catfishes, however the most generalized condition is the presence of simple sensory canals. Branching of the canals is observed during growth in some catfishes; this condition is a synapomorphy of [*Parapimelodus* + [*Bagre* + *Galeichthys*]] (Fig. 46A). A reduction in sections of the cephalic sensory canals is characteristic of some catfishes such as trichomycterids, in which complete sections of the lateral line system are lost (e.g., preopercular, mandibular, and supraorbital canals [Baskin 1973, Pinna 1988, Arratia 1990b]).

 64) Cephalic sensory canals:

  0: simple

  1: branched

C h a r a c t e r 65. The presence of integumentary teeth on the outside surface of the body is a synapomorphy of [*Nematogenys* + *Trichomycterus*] (Fig. 46A). This cha-

racter is not unique to these forms, but a synapomorphy of the loricarioids (Baskin 1973, Howes 1983b).

    65) Integumentary teeth on the outside surface of the body:
        0: absent
        1: present

C h a r a c t e r 66. The common condition among catfishes is the absence of supraneural bones. The Diplomystidae have a supraneural; however different conditions are observed in diplomystids: character 66[2] is found in some individuals of *Olivaichthys viedmensis*, and in all studied individuals of *Diplomystes camposensis* and *D. nahuelbutaensis*. Character 66[3] is observed in most studied specimens of *Olivaichthys* and also in *Diplomystes chilensis*.

The presence of a single small, ossified supraneural is an autapomorphy of Diplomystidae. The presence of a compound element or of two separate elements in *Diplomystes chilensis* and *Olivaichthys viedmensis* is a synapomorphy shared by these two species. The absence of the bone is a synapomorphy of the Siluroidea.

    66) Supraneural above the Weberian apparatus in adults:
        0: present as one single, large element
        1: absent
        2: present as one single, small element
        3: present as one element with two ossification centers or two separate elements

C h a r a c t e r 67. A supraneural that articulates with the claustrum is the primitive condition present in characiforms (Weitzman 1962, Fink & Fink 1981) and in *Olivaichthys viedmensis*. In the latter, the supraneural and claustrum contact and articulate during growth. In addition, the increased growth of the claustrum dorsally in *Olivaichthys viedmensis* separates the supraneural from the cranial occipital region.

The presence of a supraneural that does not articulate with the claustrum is a synapomorphy of the Diplomystidae, whereas the articulation between these bones present in *Olivaichthys* is an autapomorphy of this genus.

    67) Supraneural:
        0: articulates with claustrum
        1: does not articulate with claustrum

C h a r a c t e r 68. A short (e.g., *Nematogenys*) or a rudimentary lateral line in trichomycterines (Arratia & Menu Marque 1984, Arratia 1987a) is a synapomorphy of [*Nematogenys* + *Trichomycterus*].

    68) Lateral line:
        0: complete
        1: short or reduced

Characters 69 to 75 are synapomorphous features of catfishes according to the previous analysis (pp. 86—107).

C h a r a c t e r 69. Palatoquadrate that is separated into the pars autopalatina and pars

pterygoquadrata:

> 0: absent
>
> 1: present

C h a r a c t e r 70. Pterygoquadrate fused with the cartilaginous hyo-symplectic:

> 0: absent
>
> 1: present

C h a r a c t e r 71. Articulation between the autopalatine and lateral ethmoid at about the midlength of the autopalatine:

> 0: absent
>
> 1: present

C h a r a c t e r 72. Metapterygoid anterodorsal to the quadrate and forming part of the ventrolateral border of the suspensorium:

> 0: absent
>
> 1: present

C h a r a c t e r 73. Posteroventral process of quadrate:

> 0: present
>
> 1: absent

C h a r a c t e r 74. Quadrate and hyomandibula that are sutured to the preopercle:

> 0: absent
>
> 1: present

C h a r a c t e r 75. Bony symplectic:

> 0: present
>
> 1: absent

Results

Two analyses were performed using the 75 characters listed above and their character states listed in Appendix 2. The first analysis was done with all characters as ordered, except for characters 1, 5, 7, 9, 47, 63, and 66 (Fig. 46A—C). The second analysis considered all characters as unordered (Fig. 47A—E). Both analyses are identical in the phylogenetic position of the taxa; the differences are due to the unresolved relationships among diplomystids (compare Figs. 46A, 47A).

Figure 46A corresponds to the consensus of two equally parsimonious trees (consistency index = 0.672) at 137 evolutionary steps. The consensus shows the sequence from characiforms + gymnotoids (outgroup) at the base, to *Bagre* and *Galeichthys*.

Node B corresponds to the branching between the diplomystids and the [†*Hypsidoris* + Siluroidea]: This node is supported by 16 characters: 11 characters are uniquely derived, whereas five characters are homoplastic (Fig. 46A). Node C corresponds to the trichotomy among diplomystid species. This node is supported by nine uniquely derived characters and eight homoplastic ones (Fig. 46A). Node D corresponds to the branching between *Diplomystes chilensis* and *Olivaichthys*. This node is supported by two homoplastic characters (46[2] and 66[3]). *Diplomystes camposensis* and *D. nahuelbutaensis* are characterized by one autapomorphy (44[1] and 4[1]), respectively. *D. chilensis* is characterized by one homoplastic character (45[0]). *Olivaichthys viedmensis*

is characterized by six homoplastic characters (2[2], 20[1], 21[1], 24[1], 58[1], and 67[0]) (Fig. 46A). The polytomy among diplomystids in this analysis is due to the unresolved position of *Diplomystes camposensis* as the plesiomorphic sister group of the remaining diplomystids (Fig. 46B) or *D. nahuelbutaensis* as the plesiomorphic one (Fig. 46C).

Node E corresponds to the branching between †*Hypsidoris* and Siluroidea. Node E is supported by five uniquely derived characters. †*Hypsidoris* is characterized by two derived characters (1[2] and 5[1]) and five homoplasies (2[2], 16[1], 39[1], 41[1], and 55[1]).

Node F corresponds to the branching of [*Nematogenys* + *Trichomycterus*] and more derived catfishes. Node F is supported by eight uniquely derived characters and two homoplastic ones.

Node G corresponding to the branching of *Nematogenys* and *Trichomycterus*: This node is supported by six uniquely derived characters (Fig. 46A). *Nematogenys* is characterized by one autapomorphy (12[1]) and three homoplastic characters (24[1], 28[1], and 34[1]). *Trichomycterus* is characterized by four unique derived characters (47[2], 48[2], 56[2], and 62[1]) and seven homoplastic characters (13[1], 15[1], 23[1], 36[0], 41[1], 57[2], and 64[1]). All of these features are characters of trichomycterines or trichomycterids. No derived character is known for the genus *Trichomycterus* (Arratia 1990b).

Node H corresponds to the branching between ictalurids and more advanced catfishes. It is supported by three derived characters and six homoplasies (Fig. 46A). Node I corresponds to the branching between *Pylodictis* and *Ictalurus*: Node I is supported by one uniquely derived character and four homoplastic ones. *Ictalurus* is characterized by two homoplastic characters (30[1] and 42[1]).

Node J corresponds to the branching between *Heptapterus* and [*Rhamdia* + [*Parapimelodus* + [*Bagre* + *Galeichthys*]]]: Node J is supported by five homoplastic characters (Fig. 46A). *Heptapterus* is characterized by three homoplastic features (13[1], 59[0], and 61[1]).

Node K corresponds to the branching between *Rhamdia* and [*Parapimelodus* + [*Bagre* + *Galeichthys*]]. Node K is supported by one uniquely derived character and one homoplastic character (Fig. 46A). *Rhamdia* is characterized by one homoplastic character (14[1]).

Node L corresponds to the branching between *Parapimelodus* and [*Bagre* + *Galeichthys*]. Node L is supported by one uniquely derived character and four homoplastic ones.

Node M corresponds to the branching between *Bagre* and *Galeichthys*. Node M is supported by five homoplastic characters. *Galeichthys* is characterized by one reversal, character 37[0].

Second cladistic analysis

The relationships among primitive catfishes were evaluated on the basis of the 75 characters listed above and in Appendix 2. All variable characters of Diplomystidae are

considered in this analysis as bearing only their primitive states. For example, characters 16[0] and 44[1] in *Diplomystes camposensis*; characters 16[0] and 66[2] in *D. chilensis*; characters 15[0], 21[0], 24[0], 42[0], and 66[2] in *Olivaichthys viedmensis*. All characters are ordered, except characters 1, 5, 7, 9, 47, 63, and 66.

Results

Figure 50A corresponds to the consensus tree of four equally parsimonious trees at 256 evolutionary steps (consistency index = 0.656). The topology of the consensus tree is identical to that in figure 46A, except for the arrangement of the taxa within Diplomystidae. Node C (Fig. 50A) shows the unresolved relationships among the diplomystids as represented by figures 50B—E.

Only one tree is generated when the 75 characters listed above and in Appendix 2 are run as unordered (consistency index = 0.695; tree length = 131). The tree has the same arrangement of taxa, except among diplomystids, where *Olivaichthys* appears as the plesiomorphic sister group of *Diplomystes chilensis* + [*D. camposensis* + *D. nahuelbutaensis*].

Overall Results

The comparison between both trees (Figs. 46A & 50A) reveals that variable characters are capable of modifying tree topology. In both trees, the differences are at the level of the Diplomystidae. In figure 46A the most primitive diplomystids are *Diplomystes camposensis* and *D. nahuelbutaensis*, whereas *Olivaichthys* is the most primitive diplomystid or it is a polytomy among diplomystids (Fig. 50A—D) when variable taxa are considered to only exhibit the primitive state. Variation may be crucial in the understanding of relationships of catfishes, because variation is known from many structures among catfishes (e.g., Regan 1911, Alexander 1965, Lundberg & Baskin 1969, Lundberg 1982, Arratia 1982, 1983, 1987a, Arratia & Menu Marque 1981, 1984, Arratia & Schultze 1990).

Both analyses (Figs. 46A, 50A) support Grande's (1987) arrangement of the higher categories of catfishes, his Siluriformes, Siluroidei, †Hypsidoroidea, and Siluroidea. The present study provides additional characters supporting them (see below).

Chardon (1968) proposed the suborder Bagroidei with nine superfamilies; among them, the superfamily Bagroidae includes Bagridae, Pimelodidae, Ictaluridae, Ariidae and Olyridae. Several characters proposed by Chardon (1968) as diagnostic for Bagroidae are primitive or homoplastic and in addition, the monophyly of the Bagroidae has not yet been demonstrated. According to the present study, Bagroidae is supported by nine synapomorphies (Fig. 46A: Node H). The synapomorphies are: the presence of a rod-like autopalatine (not unique to Bagroidae); no articulation present between auto-palatine and vomer, the 'entopterygoid' attached by ligaments and/or connective tissue to the lateral ethmoid; metapterygoid²'entopterygoid' ligament present; hyomandibula articulating with autosphenotic and prootic; presence of the prootic as one of the bones framing the hyomandibular fossa; membranous bony extension over the ventral surface of the fifth centrum present; suture between pterosphenoid and parasphenoid present;
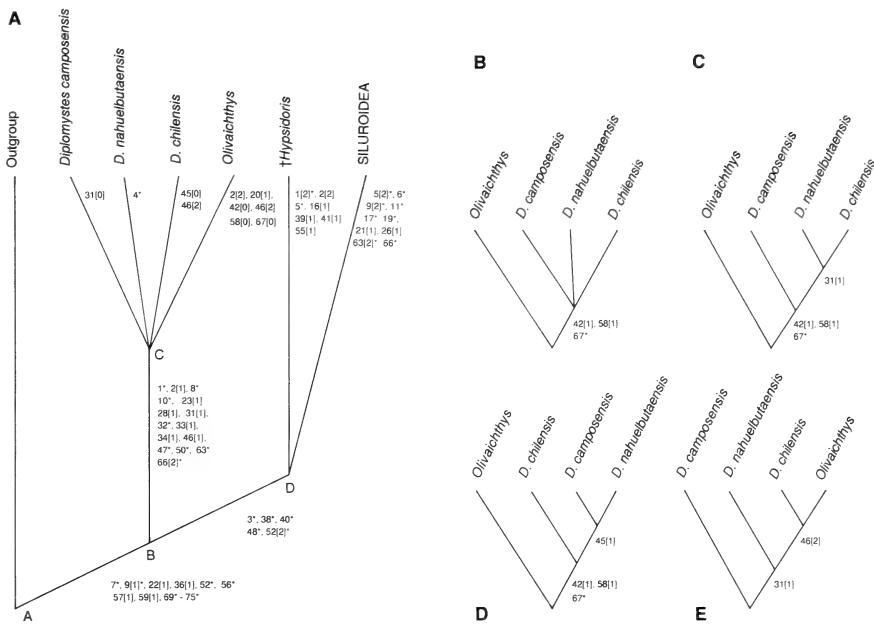
Fig.50: Hypothesis of phylogenetic relationships of certain primitive catfishes based on 75 morphological characters. All characters are ordered with exception of characters 1, 5, 7, 9, 47, 63, and 66. Characters are explained in the text; for character states see Appendix 2; however, character of Diplomystidae are considered as bearing only their primitive character states. Homoplasies are presented by their character states, but an asterisk represents a unique derived character. — A: Consensus tree of four equally parsimonious trees (consensus index 0.656); B—E: Topologies showing probable phylogenetic relationships among diplomystids.

and blood vessels partially surrounded by lamellar walls in the ventral part of the Weberian apparatus. Among the Bagroidae, the 'Pimelodidae' is not a monophyletic group, and the monophyly of the Bagridae has not been demonstrated yet. In addition, 'pimelodids', 'bagrids', and ariids are poorly known.

CONCLUSIONS

Early ontogeny

Dermal bones are the first to ossify in ostariophysans as well as in other teleosts (e.g., in 5.5 mm total length *Noturus hildebrandi* the cleithrum is ossified, and in a 6 mm specimen of *Trichomycterus areolatus* the cleithrum, premaxilla, dentary, and preopercle are visible) (Arratia & Schultze 1990). The only sure recognition of cartilage bones may be achieved using growth series; there is no way to distinguish between dermal and membrane bones. It is only by convention that a researcher accepts the definition of dermal and membrane bones by Patterson (1977).

The growth of bones from the palatoquadrate and hyo-symplectic cartilages results

largely from perichondral ossifications in all of the teleosts that I have studied (see Arratia & Schultze 1991). However, in catfishes the bones mostly enlarge through the appearance and expansion of membranous outgrowths. Jollie (1986: 371) stated that the metapterygoid is essentially dermal with no apparent chondral process; this statement is surprising considering that the metapterygoid arises from the palatoquadrate cartilage.

The study of ontogenetic series is not only helpful in testing homologies or for determination of primitive states of characters as suggested by Nelson (1978, 1985) and Mabee (1987, 1989), but it also provides a set of characters useful in taxonomy and for evaluating phylogenetic relationships. For example, characters representing early ontogenetic conditions are synapomorphies of the catfishes (1—4) and Characiformes (5).

(1) Posterior part of the palatoquadrate, the pterygoquadrate, fused with the hyo-symplectic cartilage;
(2) palatoquadrate divided into a pars autopalatina and a pars pterygoquadrata;
(3) posterior part of the autopalatine not contacting the pars pterygoquadrata through cartilage;
(4) the fusion of the pterygoquadrate and hyo-symplectic to produce a special alignment of the bones of the suspensorium during growth; and
(5) posterodorsal portion of the palatoquadrate bifid.

Some morphological characters may change during ontogeny. The sequence of the changes and/or the ontogenetic transformations are also useful characters. For example,

(1) a subautopalatine toothplate is absent early in the ontogeny of diplomystids; however, the toothplate appears later in the ontogeny in *Olivaichthys* and *Diplomystes chilensis* and
(2) the anterior part of the autopalatine is bifid early in the ontogeny of diplomystids; however, both processes become fused during the growth of *Olivaichthys* and *Diplomystes chilensis*, yet both processes remain independent of one another in *D. camposensis* and *D. nahuelbutaensis*.

Homology of chondral bones of the suspensorium

The changes in position and shape of the bones of the suspensorium may be associated to the movement of the maxillary and nasal barbels (when present), in addition to the compression or depression of the head observed in many catfishes. These changes affect all elements of the suspensorium. The chondral elements of the suspensorium of catfishes are highly modified both in shape and in position when compared with other teleosts. For example, the hyomandibula occupies the position of the metapterygoid of other teleosts, whereas the metapterygoid occupies the position of both the ectopterygoid and the entopterygoid, or of just the entopterygoid. Despite these differences, the autopalatine, metapterygoid, quadrate, and hyomandibula are homologous in teleosts.

There is no ontogenetic evidence, in any of the catfishes examined, that the hyomandibula and/or metapterygoid, and autopalatine are compound elements (contra Howes & Teugels 1989 and Howes & Ayanomiya Fumihito 1991, respectively).

Homology of entopterygoid and 'entopterygoid'

The entopterygoid is a small dermal bone that may or may not be present in diplomystids. The diplomystid dermal entopterygoid is homologous with that of other teleosts and non-teleostean fishes (Arratia & Schultze 1991). The 'entopterygoid' is a tendon bone by origin and a sesamoidal element connected by ligaments to other bones of the suspensorium and cranial elements, unlike the dermal entopterygoid.

'Entopterygoid' type 1, occasionally present in *Olivaichthys*, is a new formation. 'Entopterygoid' type 1 and a dermal entopterygoid are both present in a single individual, therefore the two elements are non-homologous.

According to the distribution of this character (Fig. 51) among catfishes, the 'entopterygoid' (except for 'entopterygoid' type 1) is homologous with the entopterygoid present in diplomystids. For such a scheme of homology to be true, I have had to assume that †*Hypsidoris* had either a entopterygoid or an 'entopterygoid', or that the loss of one or another bone in †*Hypsidoris* is an autapomorphy of this fish.

The 'entopterygoid' has a variety of ligamentous connections in catfishes (Fig. 2B—G); it is very probable that more patterns will be added to figure 2A—G as more catfishes are studied. The diversity of ligamentous connections of the 'entopterygoid' may be useful for taxonomic and phylogenetic purposes in catfishes.
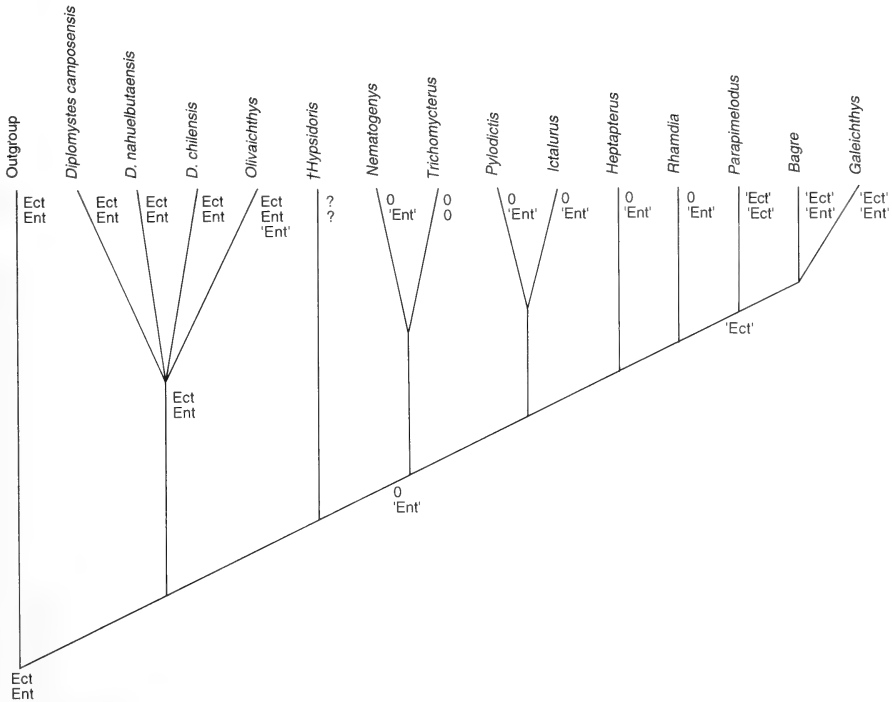
Fig.51: Distribution of certain palatal bones in catfishes. — Entopterygoid (Ent) and 'entopterygoid' ('Ent'); ectopterygoid (Ect) and 'ectopterygoid' ('Ect'). 0 = absence of the bone; ?: unknown condition.

Homology of ectopterygoid and 'ectopterygoid'

A dermal ectopterygoid is present only in diplomystids among the catfishes (Fig. 51). The diplomystid dermal ectopterygoid is homologous with that of other teleosts and non-teleostean fishes (Arratia & Schultze 1991). The presence of the 'ectopterygoid' type 1 present in catfishes such as some 'pimelodids', 'bagrids', and ariids is interpreted here as a new formation because this tendon bone is absent in the ancestor of these groups.

Homology of certain ligaments

A ligament that extends between the 'entopterygoid' and metapterygoid (Fig. 2B—G) is present in members of Siluroidea; according to the hypothesis of relationships presented herein, it is homologous among them. Within loricarioids, it is absent in trichomycterids as well as more advanced forms.

A ligament that extends between 'entopterygoid' and lateral ethmoid (Fig. 2B—G) is present in Siluroidea, but it is absent in advanced members that lack the 'entopterygoid'.

A ligament that extends between 'entopterygoid' and vomer is present in members of Siluroidea, but it is lost in several catfishes such as trichomycterids and more advanced loricarioids, *Parapimelodus*, and schilbeids (Fig. 2B—G).

The presence of the autopalatine-metapterygoid ligament is a synapomorphy of catfishes. I consider the appearance of the 'ectopterygoid' within this ligament and its separation into two ligaments (Fig. 2E, F) as an evolutionary transformation of the autopalatine-metapterygoid ligament; therefore, the autopalatine-'ectopterygoid' ligament and the 'ectopterygoid'-metapterygoid ligament are homologous with the autopalatine-metapterygoid ligament.

Diversity of bones of the suspensorium

The most primitive pattern of the suspensorium of catfishes is that of diplomystids, which in addition to the autopalatine, metapterygoid, quadrate, and hyomandibula, have both a small ectopterygoid and an entopterygoid. Although six elements may also be present in other catfishes, there is variation in the non-chondral elements. For example, six bones are present in the suspensorium of *Parapimelodus, Bagre*, and *Galeichthys*, however they do not have a dermal ectopterygoid; instead they have a specialized sesamoid 'ectopterygoid'. In addition, they lack a dermal entopterygoid, but they have a sesamoid 'entopterygoid'. Therefore, the same number of bones (six) present in the suspensorium of diplomystids and some 'pimelodids', 'bagrids', and ariids does not correspond to the same elements by ontogenetic origin.

A more specialized pattern within the suspensorium is present in ictalurids. Ictalurids (e.g., *Pylodictis, Ictalurus, Noturus*) have five bones. They have lost the dermal ectopterygoid and/or sesamoid 'ectopterygoid'; and instead of a dermal entopterygoid they have a sesamoid 'entopterygoid'. Another specialized pattern that represents an increased loss of elements is that present in trichomycterines. Trichomycterines have four

bones in the suspensorium; they do not have a dermal or sesamoid ectopterygoid or entopterygoid.

The diversity of the suspensorium of catfishes affects not only the number of bones, but also the ligamentous links between the remaining bones. For example, ictalurids have five bones in the suspensorium, and at least two patterns of ligamentous connections are known. 'Entopterygoid' type 4 is found in *Noturus* (Fig. 2D) and 'entopterygoid' type 7 (Fig. 2G) is found in *Pylodictis* and a few species of *Ictalurus*. A more complex ligamentous pattern is present in *Ameiurus melas*. The study of the variation in the ligamentous connections of the sesamoid 'entopterygoid' and the 'ectopterygoid' in catfishes is necessary to our understanding of the evolutionary transformations of the suspensorium of siluriforms.

Variation

Variability in bones, muscles, and ligamentous connections is commonly present in the suspensorium of catfishes. The variation may be ontogenetic or may only affect adult individuals and varies both intraspecifically or interspecifically.

The high degree of variation present in the Diplomystidae (Arratia 1987a; present paper) is critical because the Diplomystidae are considered to be the most primitive family within the Siluriformes. The determination of the most plesiomorphic species of diplomystid varies according to whether the primitive or apomorphic states of certain characters are considered in cladistic analyses. Thus, *Olivaichthys viedmensis* is the most primitive diplomystid when only the plesiomorphic states of variable characters are considered (Arratia 1987a; present paper: Fig. 50B—D). The scheme of relationships among diplomystids changes when only the apomorphic states of variable characters are considered (Fig. 46A). Based on these results, I advocate the description and evaluation of the variation in other catfishes so that we may understand its role within species and among catfish subgroups.

The suspensorium of ostariophysans

Fink & Fink (1981) demonstrated that the major extant ostariophysan taxa are monophyletic; this is also confirmed by the present study (Fig. 45B, C). However, my results based on 37 characters of the suspensorium (Fig. 45B) show a different arrangement of the ostariophysans than that proposed by Fink & Fink (1981) and herein. The difference is the result of my having considered characters belonging to only one morphological system. The study of the suspensorium provides numerous characters supporting the monophyly of cypriniforms, gymnotoids, and catfishes. Because the last two groups are highly diverse in the evolutionary transformations of their suspensoria, however, they share only three synapomorphies (Fig. 45C).

Higher categories of Siluriformes

Grande (1987) proposed that the Siluriformes (= Siluroidei sensu Fink & Fink 1981) are divided in the suborders Diplomystoidei (sensu Chardon 1968) and Siluroidei. According to the present study, these taxa are characterized at the **primitive** level by the

following synapomorphies listed for each category (see text and Figs. 45C, 46A, 50 for additional characters). The characters may be transformed in subgroups (e.g., pairs of barbels, maxillary processes, and maxillary teeth).

S i l u r i f o r m e s : Palatoquadrate separated into pars autopalatina and pterygoquadrata. Pterygoquadrate fused with hyo-symplectic cartilage. Autopalatine broad anteriorly, narrow and elongate posteriorly. Articulation between autopalatine and maxilla, double and anteroventrally placed. Autopalatine and metapterygoid linked by a ligament or connective tissue. Metapterygoid as main support of the eye. Metapterygoid anterodorsal to quadrate and forming part of the ventrolateral border of the suspensorium. Posteroventral process of quadrate absent. Quadrate and hyomandibula sutured with preopercle. Centra 2—4 forming the complex Weberian vertebra. Small, single supraneural above the Weberian apparatus. Pectoral fin with three proximal radials. Pelvic fin with six rays. Pelvic fin with cartilaginous radial absent. Dorsal spine present.

D i p l o m y s t o i d e i : Maxilla with teeth along most of oral margin. Maxilla with two large articular facets for autopalatine, both on the single, elongate anterior process. Anterior part of autopalatine divided into two processes early in ontogeny. Autopalatine not lying on the dorsolateral aspect of premaxilla. Hinge joint between maxilla and autopalatine absent. Hyomandibula articulates bone-to-bone with pterosphenoid. Hyoideomandibularis nerve trunk lateral to hyomandibula. Coronomeckelian bone large; usually increasing in size during growth. Ossified pharyngobranchials 1 and 2 attached to epibranchial 1 and to medial aspect of hyomandibula. Sphenotic of similar length or smaller than pterotic. Rhomboidal-shaped vomer. Single, small supraneural above Weberian apparatus in adult stage. Only maxillary barbel present. (For additional characters see Arratia 1987a, and above.)
Since Diplomystoidei comprises only the family Diplomystidae, the diagnoses of both are the same.

S i l u r o i d e i (sensu Grande 1987): Maxilla with two rudimentary processes bearing small facets for articulation with autopalatine. Dorsal and ventral hypohyals of different sizes. Fifth abdominal centrum ankylosed or fused with the Weberian complex vertebra. Weberian apparatus including fusion of abdominal centra 2—5. Caudal fin with 17 or fewer principal caudal fin rays.
The Siluroidei include the superfamilies †Hypsidoroidea and Siluroidea (Grande 1987) which are characterized by the following synapomorphies listed for these categories below.

†H y p s i d o r o i d e a : Two synapomorphies (maxillary teeth anteriorly located and maxilla with two well-developed processes that separate the autopalatine and premaxilla) and five homoplastic characters (numerous maxillary tooth rows; subautopalatine toothplate present; membranous bony extension over the ventral surface of the fifth abdominal centrum; extremely high coronoid process of dentary and angular; blood

vessels in a groove partially surrounded by lamellar walls in the ventral part of the Weberian apparatus) support this fossil clade.

†Hypsidoroidea comprises only the family †Hypsidoridae, known from the genus †*Hypsidoris*. The diagnoses of the three taxa are co-extensive.

S i l u r o i d e a : Maxilla without long anterior process. Maxilla rudimentary. Articulation between autopalatine and maxilla double and lateroventral. Dermal ectopterygoid and entopterygoid absent. 'Entopterygoid' and vomer linked by ligament and/or connective tissue. Metapterygoid without notch separating processus basalis and posterodorsal part of the bone. No supraneural above Weberian apparatus in adult stage.

Among the Siluroidea, the monotypic family Nematogenyidae can be diagnosed by: the presence of an 'entopterygoid' type 2; metapterygoid, 'entopterygoid' type 2, and autopalatine all located on the same level; the division of the levator arcus palatini muscle into three portions inserting on the posterior part of the frontal and autosphenotic; a well-developed levator operculi lateral to the opercle; and a minuscule pseudobranch medially attached to the hyomandibula.

ABSTRACT

The suspensorium of ostariophysans as well as that of other teleosts is characterized by the presence of chondral elements (autopalatine, metapterygoid, and quadrate) and dermal elements (ectopterygoid and entopterygoid). The dermopalatine fused to the autopalatine present in primitive clupeocephalans is absent in ostariophysans. Tendon bone pterygoids and additional elements as toothplates may be found among catfishes. The suspensorium of cypriniforms, gymnotoids, and catfishes is highly specialized and several synapomorphies characterize each of these groups. Among the ostariophysans, gymnotoids and catfishes have very different and highly specialized suspensoria; still they share three synapomorphies — the anterior cartilage of the autopalatine or pars autopalatina does not articulate with the neurocranium, ligamentum primordiale inserts on the dorsal tip of the lower jaw, and the ectopterygoid is rudimentary or absent.

The suspensorium of catfishes is highly specialized from early in ontogeny. Differences in the palatoquadrate separate siluriforms from the other teleosts. For example, the palatoquadrate is divided into the pars autopalatina and the pars pterygoquadrata; the pars pterygoquadrata is fused to the dorsal limb of the hyoid arch to form the hyosymplectic-pterygoquadrate plate and this produces a special alignment of the suspensorium in catfishes. The bones commonly identified as the ectopterygoid and the entopterygoid in catfishes are tendon bones that are characterized by unique ligamentous connections with other bones of the suspensorium (e.g., metapterygoid) and/or cranial bones (e.g., vomer, lateral ethmoid, orbitosphenoid), and they are sesamoid elements. The sesamoid 'entopterygoid' (types 2—7) is an evolutionary transformation of the dermal entopterygoid; both bones are homologous. In contrast, the sesamoid 'ectopterygoid' present in some catfishes such as 'pimelodids', 'bagrids', and ariids is non-

homologous with the dermal ectopterygoid present in diplomystids. This is because both — a tendon bone 'ectopterygoid' and an ectopterygoid — are missing in the ancestor of 'pimelodids', 'bagrids', and ariids.

The ligamentous and/or connective tissue connections present between the 'entopterygoid' and vomer, 'entopterygoid' and lateral ethmoid, and 'entopterygoid' and metapterygoid are homologous among members of Siluroidea; one or another is lost in some advanced members of this clade. The presence of the autopalatine-metapterygoid ligament is a synapomorphy of catfishes; the division of this ligament into two due to the appearance of the calcification of the 'ectopterygoid' is considered as a derived condition. Because of their origin and distribution among catfishes, the autopalatine-'ectopterygoid' ligament and the 'ectopterygoid'-metapterygoid ligament are homologous with the autopalatine-metapterygoid ligament.

The study of the suspensorium reveals that it is difficult to understand the bony suspensorium of siluroids without ontogenetic investigations. In this way the sesamoid 'entopterygoid' and its ligamentous connections become a tool in systematic and phylogenetic interpretations. The presence of toothplates or other dermal elements should be investigated early in ontogeny to determine their early position and relationships, allowing more useful comparisons to be made.

A phylogenetic analysis based on 130 morphological characters confirms the scheme of phylogenetic relationships of ostariophysans proposed by Fink & Fink (1981). Phylogenetic analyses based on 75 morphological characters of certain primitive catfishes confirms Diplomystidae as the sistergroup of [†Hypsidoridae + Siluroidea]; among Siluroidea, nematogenyids are more primitive than ictalurids, 'pimelodids', and ariids. The characterization of the higher categories of Siluriformes sensu Grande (1987) such as the Diplomystoidei, Siluroidei, †Hypsidoroidea, and Siluroidea are analyzed and discussed. Additional diagnostic characters are provided for these clades.

ZUSAMMENFASSUNG

Das Suspensorium der Ostariophysi ist wie das anderer Teleosteer aus Knorpelelementen (Autopalatinum, Metapterygoid, und Quadratum) und dermalen Elementen (Ectopterygoid und Entopterygoid) aufgebaut. Ein mit dem Autopalatinum verschmolzenes Dermopalatinum, das primitive Clupeocephali besitzen, fehlt den Ostariophysi. Bei den Siluriformes können Pterygoide, die aus Sehnenknochen aufgebaut sind, und zusätzliche Elemente wie Zahnplatten auftreten. Das Suspensorium der Cypriniformes, Gymnotoidei und Siluroidei ist hoch spezialisiert; mehrere Synapomorphien charakterisieren jede dieser Gruppen. Innerhalb der Ostariophysi haben die Gymnotoidei und Siluroidei sehr verschiedene hoch spezialisierte Suspensoria; dennoch haben sie drei Synapomorphien gemeinsam: Der vordere Knorpel des Autopalatinums oder der Pars autopalatina artikuliert nicht mit dem Neurocranium, das primordiale Ligament inseriert an der dorsalen Spitze des Unterkiefers, und das Ectopterygoid fehlt oder ist rudimentär.

Das Suspensorium der Siluroidei ist bereits früh in der Ontogenie hoch spezialisiert.

Unterschiede im Palatoquadrat unterscheiden die Siluroidei von anderen Teleosteern. Zum Beispiel ist das Palatoquadrat unterteilt in Pars autopalatina und Pars pterygoquadrata. Die Pars pterygoquadrata ist mit dem dorsalen Arm des Hyoidbogens verschmolzen, so daß sie eine Symplectic-Pterygoquadratum-Platte bilden, wodurch das Suspensorium der Siluroidei eine besondere Anordnung erhält. Die Knochen, die gewöhnlich als Ectopterygoid und Entopterygoid der Siluroidei bezeichnet werden, sind Sehnenknochen, die durch einzigartige ligamentöse Verbindungen mit anderen Knochen des Suspensoriums gekennzeichnet sind (z.B. Metapterygoid) und/oder Kopfknochen (z.B.: Vomer, laterales Ethmoid, Orbitosphenoid); es handelt sich um Sesamknochen. Das sesamoide 'Entopterygoid' der Typen 2 bis 7 ist eine evolutive Umbildung des dermalen Entopterygoids; beide Knochen sind homolog. Im Gegensatz dazu ist das sesamoide 'Ectopterygoid', das in einigen Siluroidei wie den 'Pimelodidae', 'Bagridae' und Ariidae auftritt, nicht homolog mit dem dermalen Ectopterygoid der Diplomystidae. Dies ist aus dem Fehlen beider Knochen, des Sehnenknochen-'Ectopterygoids' und eines Ectopterygoids, bei den Vorfahren der 'Pimelodidae', 'Bagridae' und Ariidae abzuleiten.

Die ligamentösen und/oder bindegewebsartigen Verbindungen zwischen 'Entopterygoid' und Vomer, 'Entopterygoid' und lateralem Ethmoid und zwischen 'Entopterygoid' und Metapterygoid sind innerhalb der Siluroidea homolog; die eine oder andere Verbindung kann bei einigen Vertretern dieser monophyletischen Gruppe verloren gehen. Das Vorhandensein eines Ligaments zwischen Autopalatinum und Metapterygoid ist eine Synapomorphie der Siluroidei; die Aufteilung des Ligaments in zwei durch Verknöcherung des 'Ectopterygoids' ist als fortschrittliches Merkmal anzusehen. Aufgrund seines Ursprungs und der Verteilung innerhalb der Siluroidei, sind das Ligament zwischen Autopalatinum und 'Ectopterygoid' und das zwischen 'Ectopterygoid' und Metapterygoid als homolog mit dem Ligament zwischen Autopalatinum und Metapterygoid zu betrachten.

Das Studium des Suspensoriums zeigt, daß es schwierig ist, das knöcherne Suspensorium ohne ontogenetische Untersuchungen zu verstehen. In diesem Sinne ist das sesamoide 'Ectopterygoid' und seine ligamentösen Verbindungen ein Beispiel für systematische und phylogenetische Interpretation. Das Auftreten von Zahnplatten oder anderer dermaler Elemente sollte ebenfalls auf seine frühe ontogenetische Entwicklung hin untersucht werden, um die frühe Lage und die Beziehungen dieser Elemente zu bestimmen, so daß sinnvollere Vergleiche möglich werden.

Eine phylogenetische Analyse von 130 morphologischen Merkmalen bestätigt die stammesgeschichtlichen Beziehungen der Ostariophysi, wie sie von Fink & Fink (1981) vorgeschlagen wurden. Eine phylogenetische Analyse von 75 morphologischen Merkmalen gewisser primitiver Siluroidei bestätigt die Diplomystidae als Schwestergruppe von [†Hypsidoridae + Siluroidea]; innerhalb der Siluroidea, sind die Nematogenyidae primitiver als die Ictaluridae, 'Pimelodidae' und Ariidae. Die Merkmale der höheren Einheiten der Siluriformes in Sinne von Grande (1987) wie der Diplomystoidei, Siluroidei, †Hypsidoridae und Siluroidea werden analysiert und diskutiert. Zusätzliche diagnostische Merkmale für diese monophyletischen Gruppen werden aufgeführt.

RESUMEN

El suspensorio de los ostariofisos, al igual que el suspensorio de otros teleósteos, se caracteriza por la presencia de elementos condrales (autopalatino, metapterigoides y cuadrado) y dermales (ectopterigoides y entopterigoides). El dermopalatino, que se encuentra fusionado al autopalatino en clupeocéfalos primitivos, está ausente en ostariofisos. Huesos pterigoideos originados como calcificaciones de ligamentos (huesos de tendón) y elementos adicionales como placas dentadas se encuentran presente en ciertos bagres. El suspensorio de cipriniformes, gimnótidos y bagres es altamente especializado; varias sinapomorfías caracterizan a cada uno de estos grupos. Dentro de los ostariofisos, los bagrès y gimnótidos tienen los suspensorios mas diversificados. Gimnótidos y bagres comparten tres sinapomorfías: el cartílago anterior del autopalatino o pars autopalatina no está articulado al neurocráneo, el ligamentum primordiale inserta en el extremo dorsal de la mandíbula inferior y el ectopterigoides está ausente en la mayoría de ellos.

El suspensorio de los bagres es especializado desde estados tempranos de la ontogenia. Diferencias en el palatocuadrado (cartilaginoso) separan a los bagres de otros teleósteos. Por ejemplo: el palatocuadrado de los bagres está dividido en dos secciones que son la pars autopalatina y pars pterygoquadrata. La pars pterygoquadrata se fusiona al miembro dorsal del arco hioídeo formando el cartílago hio-simplectico-pterigocuadrado; esta fusión produce una orientación espacial especial del suspensorio de los bagres. Los huesos que comunmente se han identificado como el ectopterigoides o pterigoides y el entopterigoides o mesopterigoides en bagres son calcificaciones de ligamentos (huesos de tendón); estos huesos se caracterizan por sus relaciones ligamentosas con otros huesos del suspensorio como por ejemplo el metapterigoides y/o con huesos craneanos como por ejemplo el vomer, orbitoesfenoides y el etmoides lateral; debido a sus relaciones ligamentosas estos huesos son considerados como huesos sesamoídeos. El 'entopterigoides' o entopterigoides sesamoídeo, es interpretado como una transformación evolutiva del entopterigoides dermal; ambos huesos son homólogos entre si. El ectopterigoides sesamoídeo que se encuentra presente en ciertos bagres como 'pimelódidos', 'bágridos' y áridos no es homólogo con el ectopterigoides dermal presente en diplomystidos. Esta no-homología es debida a la ausencia de un 'ectopterigoides' o ectopterigoides en los posibles antecesores de 'pimelódidos', 'bágridos' y áridos.

Las conecciones ligamentosas y/o a través de tejidos conjuntivos presentes entre el 'entopterigoides' y vomer, 'entopterigoides' y etmoides lateral y 'entopterigoides' y metapterigoides son homólogas a través de miembros de Siluroidea; una u otra conección se pierde en algunos taxones avanzados de Siluroidea. La presencia del ligamento autopalatino-metapterigoides es una sinapomorfía de los bagres; la división de este ligamento en dos ligamentos debido a la aparición de la calcificación del 'ectopterigoides' es considerado como un caracter apomórfico. Debido a su origen (división del ligamento autopalatino-metapterigoides) y a su distribución en bagres, los ligamentos autopalatino-'ectopterigoides' y 'ectopterigoides'-metapterigoides son homólogos con el ligamento autopalatino-metapterigoides.

El estudio del suspensorio muestra que es difícil entender esta estructura en bagres en

ausencia de investigaciones ontogenéticas. Estudios del desarrollo muestran que las conecciones ligamentosas del 'entopterigoides' pueden proporcionar caracteres útiles en interpretaciones taxonómicas y filogenéticas. La presencia de placas dentadas u otros elementos dermales que se encuentran en ciertos bagres, deben investigarse desde estados ontogenéticos tempranos para determinar su posición y relaciones con otros elementos y sus variaciones a través del crecimiento; esto permitirá hacer comparaciones mas útiles.

El analisis filogenético basado en 130 caracteres morfológicos confirma el esquema de relaciones filogenéticas de los ostariofisos propuesto por Fink & Fink (1981). Análisis filogenéticos basados en 75 caracteres morfológicos de ciertos bagres primitivos confirma a Diplomystidae como el grupo hermano de la clade [†Hypsidoridae + Siluroidea]; dentro de Siluroidea, nematogénidos son mas primitivos que ictalúridos, 'pimelódidos' y áridos.

Se presenta y se discute la caracterización de categorías superiores tales como Diplomystoidei, Siluroidei (sensu Grande 1987), †Hypsidoroidea y Siluroidea. Se proveen caracteres diagnósticos adicionales de estos taxones.

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Appendix 1: Character states of 130 characters of the suspensorium and other morphological structures in ostariophysans. For explanation see pp 86—107.

Characters

```
                 1111111111222222222233333333334444444444
 1234567890123456789012345678901234567890123456789
```

Outgroup	000000000?0000000000000000000000000000000000000000
Gonorynchiformes	0000010100001000000000000000000000000000011100001
Cypriniformes	0001000100100000111000000000010020000100001100000
Characiformes	0001000100000000000000000001010000000011001110100
Siluroidei	2112000101010111000110110011101111011011101111110
Gynotoidei	1000101111222000000101001100000120100011101110110

Characters

```
 5555555555566666666666777777777788888888889999999999
 01234567890123456789012345678901234567890123456789
```

Outgroup	000000000000000000000000000000000000000000?0000000000
Gonorynchiformes	00000001001101111000011111110000000000000000000000
Cypriniformes	00000010011100110101111111101101000000001001100100
Characiformes	10000000101010000000011111101111111001101100110100
Siluroidei	11111100111000100110011111101111111111110010111111
Gynotoidei	11110100101000100110011111101011111101101100110110

Characters

```
 1111111111111111111111111111111
 0000000000111111111122222222223
 0123456789012345678901234567890
```

Outgroup	000000000000000000?0?0?00000000
Gonorynchiformes	00000100000000000011000011100000
Cypriniformes	00000100000000000011011011000001
Characiformes	00000010000000000001111001100011
Siluroidei	111111110110001010101111111??00111
Gynotoidei	010100111111111111111111100011001

Appendix 2: Character states of 75 morphological characters in siluriforms. For explanation of characters see pp 108–126.

Characters

```
          1111111111111111111122222222223333333333333344444444445555555555666666666677777
 123456789012345678901234567890123456789012345678901234567890123456789012345
```

Taxon	Character states
Outgroup	000000000000000000000000000000000000000000000000000000000000000000000000000
Bagre	001021202010000001111101101010101010010111111000?000100130021111110211?01111111
Diplomystes camposensis	110000111100000100000110000100001101000000101111001010001111000100210111111111
Diplomystes chilensis	1100001111000001000001100001000011010000000210010001010001111000100310111111111
Diplomystes nahuelbutaensis	110100111100000000000110000000011011110100001001100101000111000100210111111111
Galeichthys	001021202010000001111101101010101010010111000100013002111110210102?01111111
Heptapterus	00102120020101102010111001100010000010111100101102001110110200120011?01111111
†*Hypsidoris*	22101012??0?2?0??????2??00?0?00??101111100??0?2?01??1000???0?????2???111111
Ictalurus	001021202010012010111101011110001101010100011000100120011011000200120011?01111111
Nematogenys	00102110201100001010101010100010101000101010010012110110110201??111111111
Olivaichthys	1200001111000001000100011110010001111010100010001210010001010000100300111111111
Parapimelodus	00102120020101020111000011011010011000110100101111000100030021111110210102?01111111
Pylodictis	001021200201001201011110101110001101010100011000100120011011000200120011?01111111
Rhamdia	0010212002010012010111001100010000010111100101110001000030011111100200120011?01111111
Trichomycterus	001021102010101010101??11001000000000000000221012110222101112111?11111111

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Cyrtodiopsis whitei Curran (Diopsidae, Diptera)
unter besonderer Berücksichtigung
der inneren weiblichen Geschlechtsorgane

von

MARION KOTRBA

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1993

Inhalt

„The genitalia of insects are as vital to the race as the mouthparts are to the individual. ... These organs have had to respond to all the changes of form, habits and habitats of the organism, as well as to physiological differences, and it is our duty to interpret them as adaptions to function, even if we describe them in terms of morphology, the same as we have done with the mouthparts. If we do this, I believe we shall add greatly to the strength of the foundations of our taxonomic edifice and add enormously to the superstructure" (Muir 1930).

EINLEITUNG

Die Stielaugenfliege *Cyrtodiopsis whitei* Curran, 1936 (Diopsidae, Diptera) (Abb.1) ist im tropischen Regenwald Malaysias beheimatet. Dort ist sie tagsüber an Bachufern zu finden, nachts versammeln sich die Tiere an geschützt herabhängenden, dünnen Pflanzenteilen zu kleinen Schlafgesellschaften. Biologie und Verhalten von *C. whitei* sind in mehreren Arbeiten von Burkhardt & de la Motte (1983a, 1983b, 1985, 1986, 1987, de la Motte & Burkhardt 1983) beschrieben.
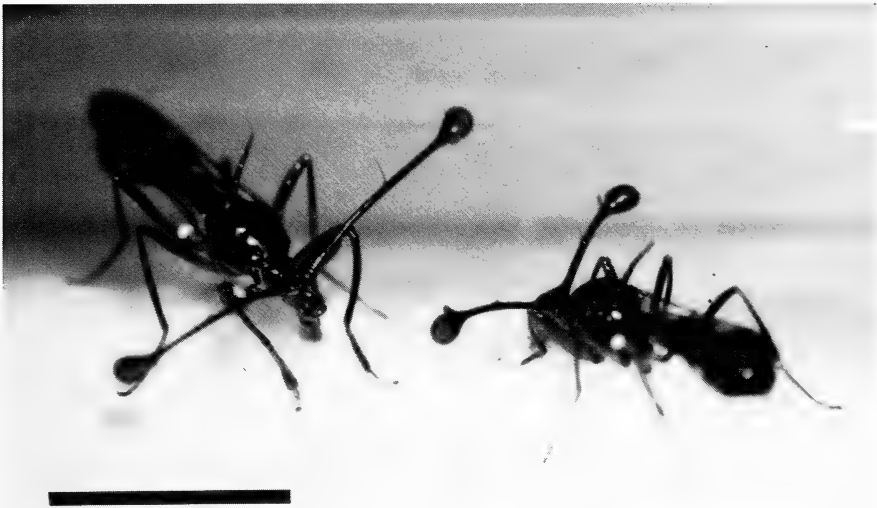
Abb.1: *Cyrtodiopsis whitei*. Im Verhältnis zur Körperlänge sind die Augenstiele großer Männchen (links) wesentlich länger als die etwa gleich großer Weibchen (rechts). Balkenlänge 5000 μm.

Bei der Forschung nach Ursprung und Funktion der langen, stark sexualdimorphen Augenstiele von *C. whitei* ist im Laufe der Jahre neben der Sehphysiologie zunehmend auch die Fortpflanzungsbiologie dieser Tiere ins Zentrum wissenschaftlichen Interesses gerückt. Bereits gut untersucht ist in diesem Zusammenhang die Bildung der Schlafgesellschaften, bei der unter anderem Konkurrenz zwischen den Männchen und weibliche Zuchtwahl eine Rolle spielen (Burkhardt & de la Motte 1987, 1988, Kotrba 1985). Die Zahl der weiblichen Schlafgenossinnen eines Männchens, wie auch die Zahl seiner Kopulationen am Schlafplatz, sind positiv mit seiner Körpergröße korreliert. Die erhöhte Kopulationsrate großer Männchen am Schlafplatz scheint allerdings unerheblich, wenn man die hohe Kopulationshäufigkeit und Promiskuität bedenkt, die tagsüber bei *C. whitei*-Weibchen beobachtet wurde (s. „Kopulation"). Notwendige Voraussetzung für eine Interpretation dieser Ergebnisse ist die Kenntnis der Vorgänge bei der Spermaübertragung und -speicherung, sowie bei der Befruchtung der Eier.

6

Obwohl einigen Diopsidenarten als Reis- bzw. Maisschädlinge wirtschaftliche Bedeutung zukommt (Feijen 1989), ist nur wenig über ihr Reproduktionssystem bekannt. Die spärliche, aus der Literatur verfügbare Information über die Geschlechtsorgane von Diopsiden (Zusammenfassung der Literatur in Feijen 1989) konzentriert sich fast ausschließlich auf äußerlich sichtbare Teile und einige wenige, stark sklerotisierte Teile im Körperinneren. Ebenso gibt es zwar einige Verhaltensbeobachtungen zu Kopulation und Eiablage, jedoch keinerlei Befunde über die inneren Vorgänge bei Spermatransfer und Befruchtung. Um diese Lücken zu schließen, wurde die Morphologie des weiblichen Reproduktionstraktes von *C. whitei* im Detail, sowie die Morphologie der Eier, der männlichen Geschlechtsorgane und der Spermatozoen untersucht. Die Vorgänge bei Kopulation und Eiablage wurden anhand von Verhaltensbeobachtungen und zu bestimmten Zeitpunkten während der untersuchten Verhaltenskontexte fixierten Präparaten rekonstruiert.

Detaillierte Angaben über Morphologie und Funktion der inneren Geschlechtsorgane liegen überhaupt erst bei wenigen acalyptraten Fliegen vor. Eine umfassende Beschreibung des Reproduktionssystems von *C. whitei* kann deshalb nicht nur zur Interpretation des artspezifischen Fortpflanzungsverhaltens, sondern auch zum Verständnis des Reproduktionsgeschehens bei den Acalyptraten im allgemeinen beitragen. Nicht zuletzt mag sie als Ausgangspunkt dienen für zukünftige Untersuchungen im Hinblick auf die Phylogenie der acalyptraten Schizophora, indem sie Merkmale der inneren weiblichen Geschlechtsorgane aufzeigt, welche sich für eine vergleichende Untersuchung anbieten, bisher aber nicht berücksichtigt wurden.

MATERIAL UND METHODEN

Die untersuchten Tiere entstammten einer Zucht an der Universität Regensburg. Dabei handelt es sich um Nachkommen von aus Malaysia eingeführten Tieren der Art *Cyrtodiopsis whitei*. Die Zucht wird alle 1—2 Jahre durch Freilandfänge aufgefrischt. Den Verhältnissen im natürlichen Habitat entsprechend, erfolgt die Haltung der Tiere bei einer Temperatur von 24—27 °C und einer relativen Luftfeuchtigkeit von ca. 85%. Ein äquatorialer Tag-Nacht-Wechsel wird durch Hell- und Dunkelperioden von je 12 Stunden Dauer simuliert.

C. whitei erreicht ca. 12 Tage nach dem Schlüpfen die Geschlechtsreife (de la Motte & Burkhardt 1983), die Lebensdauer beträgt bis zu einem Jahr (Burkhardt & de la Motte 1987). Für die vorliegenden Untersuchungen wurden 1—6 Monate alte Tiere verwendet, um zu gewährleisten, daß mit geschlechtsreifen, aber nicht überalterten Tieren gearbeitet wurde.

Sollten in den Versuchen zur Spermaübertragung jungfräuliche Weibchen eingesetzt werden, so wurden diese 1—2 Tage nach dem Schlüpfen aussortiert und bis zum Versuch in einem gesonderten Käfig gehalten. Die männlichen Versuchstiere hingegen wurden in einem Käfig mit gemischtgeschlechtlicher Population gehalten und erst wenige Tage vor dem Versuch in einem separaten Käfig isoliert, um eine Erschöpfung ihres Spermavorrats auszuschließen. Die Versuchstiere für alle anderen Untersuchungen stammten ebenfalls aus Käfigen mit gemischtgeschlechtlichen Populationen, die Weibchen waren deshalb in der Regel mehrfach begattet.

Die Versuche zur Kopulation bzw. Spermaübertragung wurden in den ersten Tagesstunden durchgeführt, da die Kopulationshäufigkeit in dieser Zeit am größten ist (Abb.34). Sollten Paare während der Kopulation fixiert werden, so wurden die Tiere in Plastikröhrchen zusammengesetzt und 15, 30 oder 40 s nach Beginn der Kopulation aus dem Röhrchen in flüssigen Stickstoff geworfen. Außerdem wurden Weibchen in verschiedenen Zeitintervallen nach einer oder mehreren Kopulationen getötet und fixiert. Die Daten zur Kopulationsaktivität im Tagesverlauf (Abb.34) stammen aus Laborversuchen, in denen Populationen aus jeweils 7 Weibchen und 5 verschieden großen Männchen an insgesamt 3 Tagen während der gesamten Helligkeitsphase beobachtet wurden (Kotrba 1985).

Zur Fixierung während der Eiablage wurden Weibchen 5—8 s nach Einnehmen der Eiablagehaltung in flüssigen Stickstoff geworfen. Die Daten zur Eiablageaktivität im Tagesverlauf (Abb.41) wurden freundlicherweise von Prof. Dr. D. Burkhardt und Dr. I. de la Motte zur Verfügung gestellt. Sie stammen aus Laborversuchen, in denen Populationen aus 6—7 Weibchen und unterschiedlich vielen Männchen an insgesamt 25 Tagen während der gesamten Helligkeitsphase beobachtet wurden.

Frisch getötete Tiere wurden in Insektenringer präpariert, fixierte Abdomina in 70%igem Ethanol. Zur Untersuchung der inneren Geschlechtsorgane wurde der gesamte Reproduktionstrakt mitsamt den anhängenden äußeren Geschlechtsorganen entnommen. Der männliche Kopulationsapparat läßt sich präparativ herausklappen,

indem man das Abdomen von ventral her eröffnet und das Phallapodem mit einer feinen Pinzette caudad bewegt. Die Darstellung der Innervierung der inneren weiblichen Geschlechtsorgane erfolgte durch Füllung mit $CoCl_2$ vom Abdominalnerv her und anschließende Silberverstärkung nach Bacon & Altman (1977). Die äußere Morphologie der Spermatozoen wurde an Zupfpräparaten von Hoden und Spermatheken untersucht, die der Eier an natürlich abgelegten und an aus Ovarien herauspräparierten Eiern. Von den Weibchen ausgeschiedene Spermatophorenhüllen konnten von den Schlaffäden abgesammelt werden.

Es wurden Totalpräparate, Dickschnitte, Semidünnschnitte und Ultradünnschnitte untersucht. Für die Lichtmikroskopie wurde je nach Anforderungen mit 70%igem Ethanol oder mit Bouin fixiert. Totalpräparate wurden mit Toluidinblau angefärbt und in Canadabalsam eingeschlossen oder zur selektiven Darstellung cuticulärer Strukturen in Polyvinyllactophenol mit einem Zusatz von Direkttiefschwarz[1]) (Streng 1976) eingeschlossen. Semidünnschnitte von in Durcupan eingebetteten Präparaten wurden nach Richardson (1960) oder nach van Even (1987) angefärbt. Zur Elektronenmikroskopie erfolgte die Fixierung nach Karnovsky (1965), für Transmissionselektronenmikroskopie außerdem eine Kontrastierung der Ultradünnschnitte nach Reynolds (1963). Eine eingehendere Beschreibung der angewandten Methoden findet sich bei Kotrba (1991).

Die relativen Lagebezeichnungen „proximal" und „distal" sind auf die Vulva bzw. das Phallotrema bezogen. Bei der Beschreibung von Zellen bzw. Zellschichten bezeichnet „basal" die dem Hämolymphraum zugewandte, „apikal" die dem Lumen zugewandte Region. Größenangaben erfolgen in der Regel gerundet. Dabei ist zu beachten, daß die Größe des gesamten Reproduktionstraktes und somit auch der einzelnen Organe individuell sehr unterschiedlich sein kann. Dort, wo zur Vergleichbarkeit mit Literaturdaten oder zu Volumensberechnungen exakte Angaben vonnöten sind, werden Mittelwert, Standardabweichung und Anzahl der Meßwerte in der Form $\overline{x}$ ($\pm$se; n) angegeben.

Bedingt durch die umfangreiche Thematik sind die Ergebnisse relativ heterogen. Teile der Diskussion, die sich auf die Interpretation einzelner Details bzw. auf den Vergleich mit Literaturdaten beziehen, sind deshalb in den Ergebnisteil integriert. Alle derartigen Aussagen sind durch die kleinere Schrift eindeutig von den Ergebnissen abgesetzt.

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[1]) Direkttiefschwarz EW CHROMA 1B 233

ERGEBNISSE

WEIBLICHES REPRODUKTIONSSYSTEM

Äußere Merkmale des weiblichen Abdomen

Das Abdomen von *Cyrtodiopsis whitei* ist lang und schlank, in etwa keulenförmig, wobei die ersten zwei Abdominalsegmente einen sehr schlanken Stiel bilden (Abb.2, 3). Ein Ovipositor ist nicht ausgebildet.
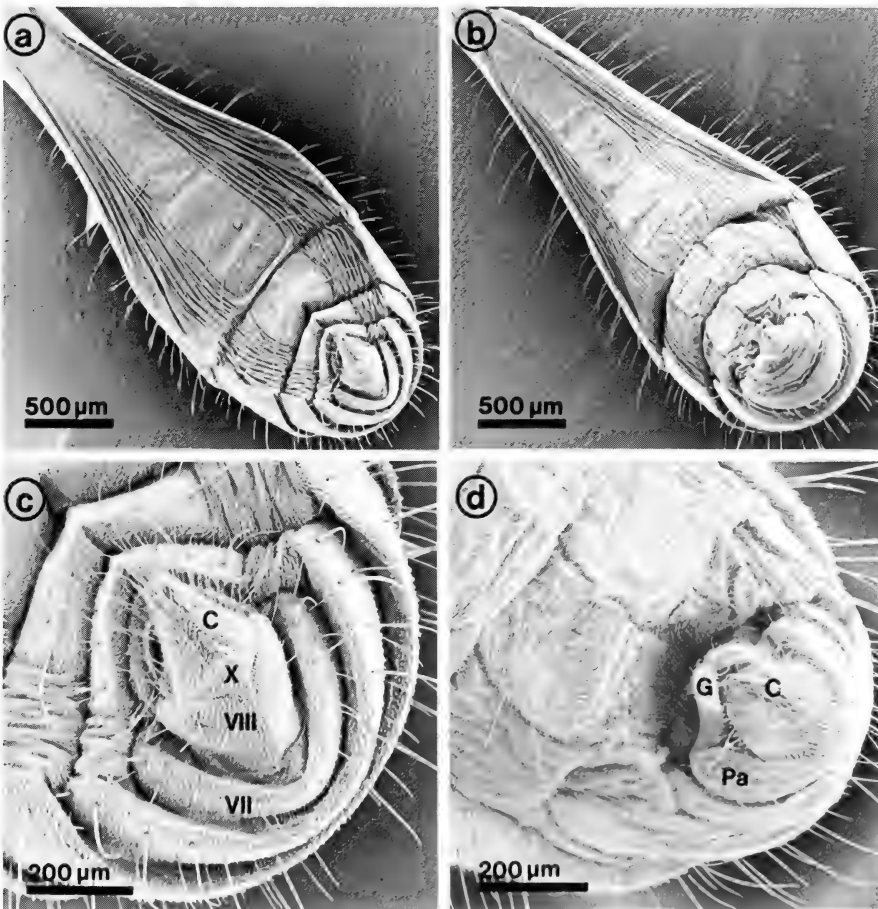
Abb.2: Abdomen von *C. whitei*, Ventralansicht, REM. (a, c) weibliches Abdomen; (b, d): männliches Abdomen.

VII: Tergum 7, VIII: Tergum 8, X: Tergum 10, C: Cercus, Pa: Periandrium, G: Gonostyli.

Die Tergite 1—3 sind zu einem Syntergit verschmolzen, die nachfolgenden Tergite 4—7 normal ausgebildet. Tergit 8 ist in zwei Platten unterteilt, die sich in der Mitte berühren. Die Sternite 1—7 (Abb.3a) sind normal ausgebildet, jedoch liegt zwischen den Sterniten 1 und 2 ein zusätzliches kleines, spangenförmiges Sklerit. Sternit 7 ist seitlich über schmale, sklerotisierte Bänder mit Tergit 7 verbunden. In diesen Bändern münden die siebenten und hintersten Abdominalstigmen, während alle vorangehenden Stigmen in der Pleuralmembran nahe dem mittleren lateralen Rand der Tergite münden. Sternum 8 ist größtenteils membranös, trägt aber an seinem caudalen Rand 2 sklerotisierte, behaarte Bereiche, die den Vorderrand der Vulva begrenzen. Das 9. Segment weist keine äußerlichen Sklerotisierungen auf. Hinter der Vulva liegt die in etwa dreieckige Subanalplatte. Sie faßt, zusammen mit dem Tergum 10 und den ventrolateral am Tergum 10 ansetzenden Cerci, den Anus ein. Die Cerci sind eingliedrig und zeigen im ausgestreckten Zustand (z. B. bei Eiablage und Kopulation) caudad. In der Ruhe wird das Abdomenende ventrad eingekrümmt, so daß die Cerci ventrad bis craniad weisen (Abb.2a).
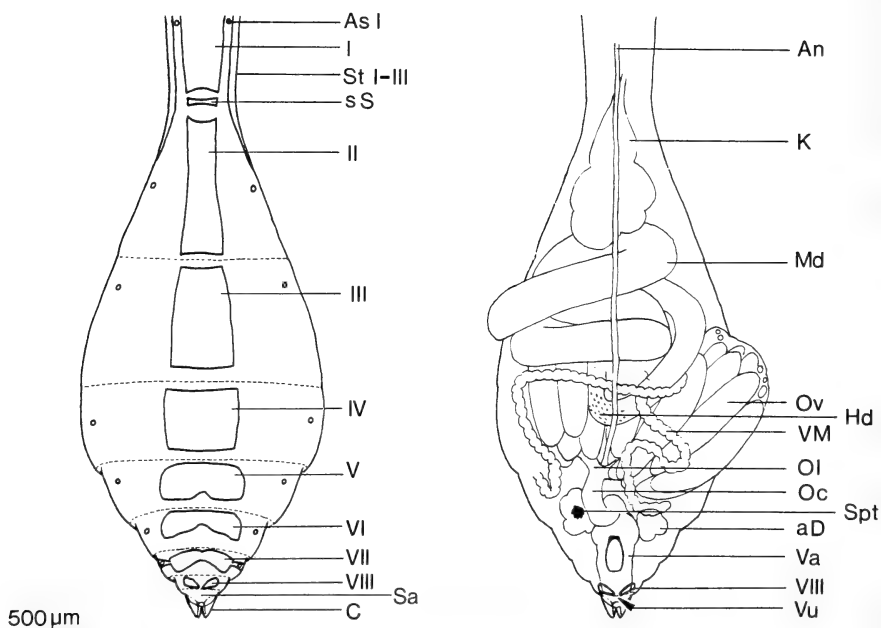
Abb.3: Weibliches Abdomen von *C. whitei*. (a) Ventralansicht; (b) ventrale Körperwand und Fettkörper entfernt.

I-VIII: Sternit 1—8, aD: akzessorische Drüse, An: Abdominalnerv, As I: 1. Abdominalstigma, C: Cercus, Hd: Hinterdarm, K: Kropf, Md: Mitteldarm, Oc: Oviductus communis, Ol: Oviductus lateralis, Ov: Ovar, Sa: Subanalplatte, Spt: Spermathek, sS: spangenförmiges Sklerit, St: Syntergum, Va: Vagina, VM: Vas Malpighii, Vu: Vulva.

In der Zählung bzw. Benennung der verschiedenen Sklerite stimmen die bisherigen Bearbeiter nicht überein. Die hier gewählte Benennung folgt Feijen (1989), der in seiner Monographie über die Diopsidae die äußere Morphologie des Diopsidenabdomens beschrieben und dabei die gesamte bisherige Diopsidenliteratur berücksichtigt hat. Die Subanalplatte entspricht nach Feijen wahrscheinlich dem Sternum 10. Ob die Bezeichnungen Tergum 10, bzw. Sternum 10 im strengen Sinne anwendbar sind, bleibt jedoch zu prüfen. Ansonsten wären die etwas weiter gefaßten Begriffe Epiproct und Hypoproct (Peterson 1987), bzw. Supraanalplatte und Subanalplatte anzuwenden.

Das Fehlen eines distinkten Tergit 9 ist bei den Cyclorrhapha die Regel (McAlpine 1981), Sternit 9 ist nach Peterson (1987) bei den Diopsidae entweder völlig membranös oder zu einer internen sklerotisierten Struktur umgebildet.

Die Subanalplatte trägt nahe dem terminalen Ende zwei median nahe beieinanderstehende Setae, die fast die Länge der Cerci erreichen (Abb.3, 44). Bei mechanischer Reizung dieser Setae stülpen die Weibchen reflexartig die Vagina etwas heraus, wobei ventral eine sklerotisierte Ringstruktur teilweise sichtbar wird. Dieses Verhalten spielt bei der Kopulation (s. dort) eine Rolle.

Situs des weiblichen Abdomen

Eröffnet man das weibliche Abdomen von ventral her (Abb.3b), so findet man unter einer Fettkörperschicht die Schlingen des Mitteldarmes, auf deren vorderem Teil der dünnwandige Kropf liegt. Der Hinterdarm, erkennbar an der Abzweigung der Malpighischen Gefäße und an den durchscheinenden Cuticulazähnchen, verschwindet zwischen den Ovarien und verläuft dorsal von Oviductus communis und Vagina zum Anus. Ventral in der Mittellinie verläuft der Abdominalnerv. Nach Entfernung von Kropf und Mitteldarm werden die Ovarien ganz sichtbar, die durch Tracheen zwischen den Mitteldarmschlingen und dem dorsalen Diaphragma verankert sind. Enthalten die Ovarien Eier, so können sie sich bis ins 3. Abdominalsegment craniad erstrecken. Die beiden lateralen Ovidukte münden in den Oviductus communis und dieser in das craniale Ende der Vagina, die in den Segmenten 6—8 liegt.

Übersicht über die inneren weiblichen Geschlechtsorgane

Von den paarigen Ovarien kommend, vereinigen sich die kurzen lateralen Ovidukte zum s-förmig gekrümmten Oviductus communis, der in das craniale Ende der muskulösen Vagina übergeht (Abb.3b, 8). In diese münden dorsal die zwei Spermathekengänge und etwas caudal davon die Ausführgänge der paarigen akzessorischen Drüsen. Der linke Spermathekengang trägt eine, der rechte zwei Spermatheken. In der ventralen Wand der Vagina liegt ein unpaares ventrales Receptaculum, welches distal in 30—40 Kammern unterteilt ist, und weiter caudal ein sklerotisierter Ring, der ein Polster aus besonders differenzierten Epithelzellen umschließt. Die Vulva mündet hinter dem Sternum 8 nach außen.

Die Literatur enthält nur wenige Befunde über die inneren weiblichen Geschlechtsorgane von Diopsiden, die über eine Beschreibung der Spermatheken hinausgehen.

Van Bruggens (1961) Zeichnungen von *Diopsis thoracica, Diopsis* cf. *circularis* und *Diasemopsis* cf. *basalis* wurden offensichtlich anhand mazerierter Präparate erstellt. Außer den Spermatheken ist jeweils eine mehr oder weniger ringförmige Struktur zu erkennen, die dem sklerotisierten Ring von *C. whitei* entsprechen dürfte. Die Form der Vagina und die Position des sklerotisierten Ringes ist nicht nachvollziehbar, ein ventrales Receptaculum und akzessorische Drüsen fehlen.

Eine realistischere Darstellung der inneren weiblichen Geschlechtsorgane von *Diopsis subnotata* stammt von Tan (1965, Fig. 73). Die Zeichnung zeigt ein unmazeriertes Totalpräparat mit einem sklerotisierten Ring in der ventralen Wand der Vagina und mit drei dorsalen Spermatheken. Akzessorische Drüsen fehlen. An der Stelle des ventralen Receptaculum ist ein schwarzer Fleck eingezeichnet. Leider wurde diese Struktur weder in der Abbildung beschriftet noch im Text erwähnt.

Kumar & Nutsugah (1976) stellen schematisch Ovarien, Vagina, drei Spermatheken und zwei akzessorische Drüsen von *Diopsis thoracica* dar. Der Text enthält kaum zusätzliche Informationen. Eine weitere Arbeit von Kumar (1978b) befaßt sich mit den weiblichen Geschlechtsorganen von *Sphyracephala hearseyana*. Hier werden Ovarien, Ovidukte, Vagina und drei Spermatheken beschrieben. Akzessorische Drüsen werden als fehlend angegeben, ein sklerotisierter Ring oder ein ventrales Receptaculum nicht erwähnt. Die Vagina mündet durch den Gonoporus in ein muskulöses Atrium, welches mit einer dicken, dornigen Intima ausgekleidet ist. Die Vulva liegt zwischen den Sterniten 7 und 8. Diese Befunde lassen sich mit den Verhältnissen bei *C. whitei* nicht vergleichen, was teilweise an der relativ entfernten Verwandschaft der beiden untersuchten Arten liegen mag.
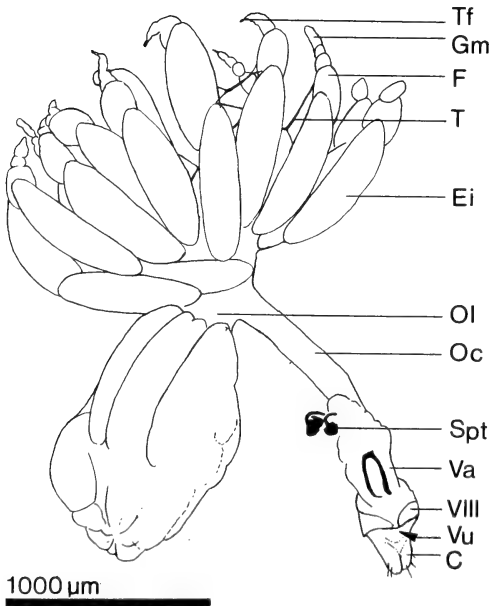
Abb.4: Innere weibliche Geschlechtsorgane von *C. whitei*, Ventralansicht, peritonealer Überzug des linken Ovars abpräpariert.

C: Cercus, Ei: reifes Ei, F: Follikel, Gm: Germarium, Oc: Oviductus communis, Ol: Oviductus lateralis, Spt: Spermathek, T: Trachee, Tf: Terminalfaden, Va: Vagina, Vu: Vulva, VIII: Sternit 8.

1000 µm

Ovarien

Die eiförmigen Ovarien können, wenn sie reife Eier enthalten, eine Länge von 1200 μm erreichen (Abb.3b, 4). Sie erstrecken sich dann vom 5. bis ins 3. Abdominalsegment. Jedes Ovar besteht aus 11—16 meroistisch polytrophen Ovariolen, wobei sich ihre Anzahl im linken und rechten Ovar meist um 1—2 unterscheidet.

Der craniale Pol der Ovarien ist abgerundet und weist kein terminales Aufhängungs-band auf. Die Ovarien sind durch Tracheen zwischen dem dorsalen Diaphragma und dem Mitteldarm aufgehängt, und feine Tracheen verbinden auch die Ovariolen unter-einander. Zusätzlich hält ein peritonealer Überzug aus netzartig verzweigten, anasto-mosierenden Muskelzellen die Ovariolen zusammen. Im Nativpräparat unter Ringer führen die Ovarien langsame Kontraktionen aus.

Jede Ovariole ist von einer geschlossenen Epithelschicht umgeben (Abb.5). Darüberhin-aus enthält die Ovariolenwand Muskelfasern, welche auch die einzelnen Ovariolen im Nativpräparat zu Kontraktionen befähigen. Das craniale Ende der Ovariole ist in dem die Ovarien umgebenden Muskelnetz über einen aus geldrollenartig übereinanderlie-genden, flachen Zellen bestehenden Terminalfaden aufgehängt. Zur Ovariole hin geht der Terminalfaden in einen größeren Klumpen scheinbar undifferenzierter Zellen über, das Germarium, welches nach proximal einzelne Follikel mit jeweils 16 Zellen ab-schnürt. Sie sind von einem hochprismatischen Follikelepithel umgeben und bleiben untereinander durch eine dem Terminalfaden ähnliche Zellsäule verbunden.

Das proximal an das Germarium anschließende Vitellarium enthält ca. 5 Follikel ver-schiedenen Alters. Je älter ein Follikel ist, desto größer ist die am proximalen Pol gele-gene Eizelle, welche die 15 Nährzellen an das terminale Ende des Follikels verdrängt. Reife Eier erscheinen durch eine in das Hohlraumsystem des Chorions (s. „Eier") einge-lagerte Gasschicht im Nativpräparat im Auflicht strahlend weiß, im Durchlicht dunkel. Proximal der letzten Eikammer, die oft ein reifes Ei enthält, liegt in der Ovariole ein Zellhaufen, der im Nativpräparat gelblich gefärbt sein kann. Die Ovariolen vereinigen sich in einem kurzen Calyx zum Oviductus lateralis (Abb.7).

Der Aufbau der Ovarien von *C. whitei* entspricht dem von früheren Autoren für andere höhere Dipteren beschriebenen (*Musca domestica* (Leydig 1867), *Drosophila melanogaster* (Miller 1965)). Nach Snodgrass (1935) repräsentiert das die Ovariolen umgebende Epithel die ursprüngliche meso-dermale Wand der Gonaden. Das Follikelepithel geht, ebenso wie der Terminalfaden, aus den Epithelzellen des Germariums hervor, und sezerniert später das Chorion (Lindner 1949, Ulrich 1963). Bei den 16 in einem Follikel enthaltenen Zellen handelt es sich jeweils um die Tochterzellen einer Oogonie, von denen sich eine zur Eizelle entwickelt, während die anderen zu Nährzellen wer-den (Gilbert 1988). Reste der Follikel- und Nährzellen eines ehemaligen Follikels bilden den von Leydig (1867) als Corpus luteum bezeichneten Zellhaufen im proximalen Ende der Ovariole.

Eier

Die Eier haben eine mittlere Länge von 841 μm ($\pm$24 μm; n=30) und eine mittlere Breite von 238 μm ($\pm$12 μm; n=30). Sie sind in etwa kahnförmig, mit abgerundeten

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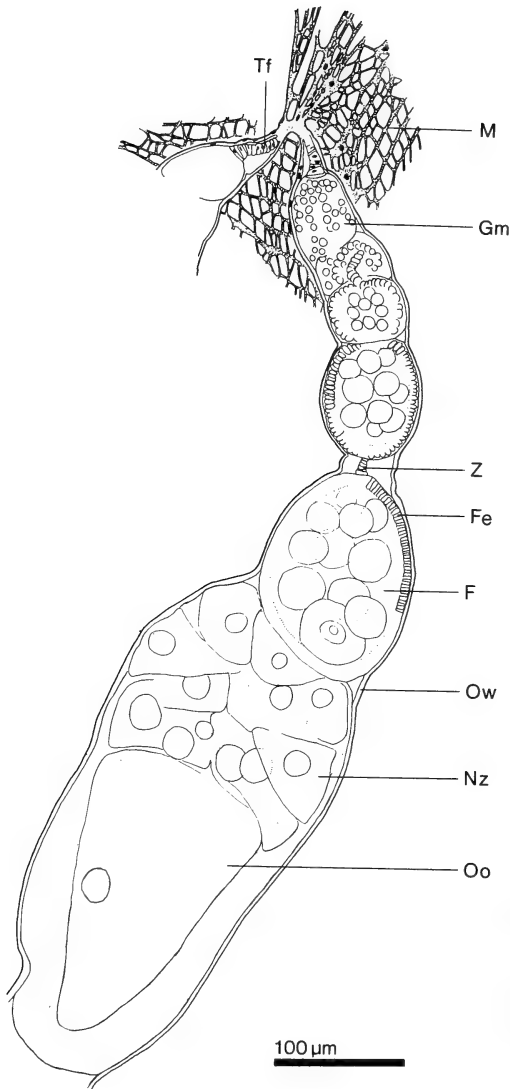
Abb.5: Ovariole von *C. whitei*, Zeichnung nach einem Nativpräparat (der letzte Follikel enthielt ein reifes Ei und wurde seiner Größe wegen nicht abgebildet).

F: Follikel, Fe: Follikelepithel, Gm: Germarium, M: Netzartiger Überzug aus anastomosierenden Muskelzellen (präparativ abgelöst), Nz: Nährzelle, Oo: Oocyte, Ow: Ovariolenwand, Tf: Terminalfaden, Z: Zellsäule.

Enden (Abb.6a). Das Ende, welches die Mikropyle trägt, erscheint etwas schlanker und stumpfer als das andere. In der Mittellinie der flacheren Oberseite des Eies verläuft ein niedriger Grat. Bei der Eiablage wird die Unterseite des Eies mit Hilfe eines Sekrets an das Substrat geklebt (Abb.6a).

Die Mikropyle liegt, nach den Verhältnissen im Ovar beurteilt, am cranialen Pol des Eies, der bei der Eiablage die Vagina zuletzt verläßt. Die einzige Öffnung der Mikropyle
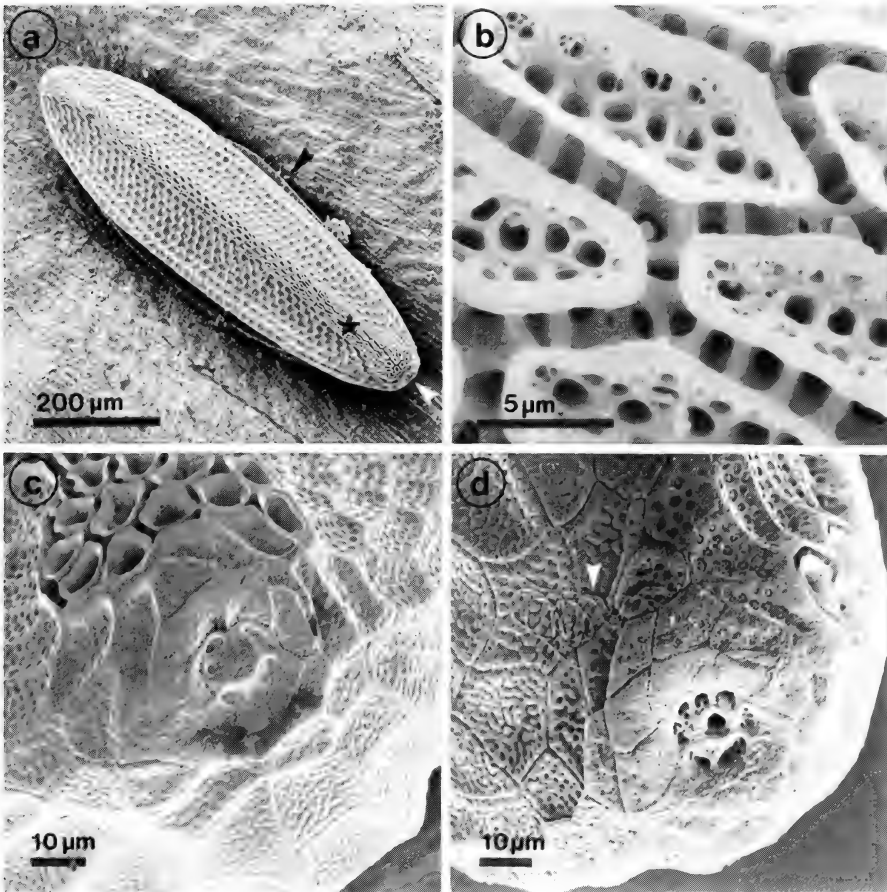
Abb.6: Ei von *C. whitei*, REM. (a) auf einem Maisblatt abgelegtes Ei, weißer Pfeil: Mikropyle, schwarzer Pfeil: Sekret, Stern: Grat; (b) Aufsicht auf die wabenartige Chorionstruktur des Grates; (c) Aufsicht auf die mit einer Sekretkappe versehene Mikropyle eines aus dem Ovar herauspräparierten Eies; (d) Aufsicht auf die offene Mikropyle eines abgelegten Eies mit aufgelagerten Spermatozoen (Pfeil).

hat einen Durchmesser von 3—4 μm (Abb.6c,d). Sie liegt im Zentrum einer radiären Speichenstruktur, die ihrerseits von einer Rosette aus schuppenförmigen Chorionplatten umgeben ist. Die Oberfläche des Grates und des runderen Eipols ist von einer wabenartigen, tief zerklüfteten Chorionstruktur bedeckt (Abb.6a,b). Sie ist stark wasserabweisend. Im REM erkennt man nebeneinanderliegende Wannen mit hohen, scharfkantigen Rändern. Der Grund der Wannen ist, ebenso wie die zwischen den Wannen liegenden tiefen Furchen, von Poren durchsetzt, deren Durchmesser bis zu 2 μm beträgt. Auch der Rest der Chorionoberfläche ist strukturiert: Die Oberseite des Eies ist beiderseits des Grates von flachen, hexagonalen Mulden bedeckt (Abb.6a), während die

Unterseite durch parallele Längsrippen unterteilt ist. Überall sind kleine Poren ausgebildet, deren Durchmesser unter 0,1 μm liegt. Alle Poren stehen mit einem gasgefüllten Hohlraumsystem im basalen Bereich des Chorions in Verbindung (Abb.15).

Im Lebensraum von *C. whitei* an Bachufern des tropischen Regenwaldes können die Eier bei Regen oder Überschwemmungen zeitweise von Wasser bedeckt sein. In Anpassung daran ist ein Plastron (Hinton 1961) ausgebildet. In dem ausgedehnten Hohlraumsystem des Chorions wird eine Gashülle festgehalten, die über zahlreiche Poren mit dem umgebenden Medium und mit der Oocyte in Gasaustausch steht. So ist auch im Falle einer Überschwemmung die Sauerstoffversorgung des Embryos gewährleistet. Die hydrophobe Oberfläche des Grates verhindert, daß Wasser in die großen Poren eindringt. Beim Trockenfallen reißt die Wasseroberfläche hier besonders früh auf, so daß der direkte Kontakt zur Luft wiederhergestellt wird.

Eine Anpassung an zeitweise Überflutung beschreibt Sen (1921) bei den Eiern von *Sphyracephala hearseyana* (Diopsidae). Nach seinen Beobachtungen schlüpften Larven sogar noch aus Eiern, die drei Wochen lang unter Wasser gehalten worden waren.

Das Ooplasma reifer Eier enthält zahlreiche Lipidtropfen und Dottervakuolen (Abb.15, 44). Auf der Cytoplasmamembran der Oocyte liegt die etwa 3 μm dicke Membrana vitellina. Ihr folgt nach außen hin die weniger als 0,5 μm dünne, innerste Schicht des Chorions („inner endochorionic layer", Degrugillier & Leopold 1976), die auch die Innenseite der Mikropyle überzieht. Die äußere, eigentliche Eischale (restliches Endo- und Exochorion) ist an der Unterseite des Eies ca. 4 μm, an der Oberseite lateral ca. 8 μm, und im Bereich des medianen Grates bis zu 12 μm dick. Das gasgefüllte Hohlraumsystem beansprucht davon jeweils ungefähr das basale Drittel. Bei Eiern, die aus dem Ovar herauspräpariert wurden, liegt über der Mikropyle eine Sekretkappe, die abgelegten Eiern fehlt (s. „Eiablage", Abb.6c,d).

Da bereits zahlreiche Arbeiten über die Ultrastruktur von Diptereneiern vorliegen, wurde hier auf eine eingehendere Untersuchung verzichtet. Eine zusammenfassende Beschreibung findet sich beispielsweise bei Margaritis (1985).

Laterale Ovidukte

Die lateralen Ovidukte sind mit weniger als 100 μm relativ kurz (Abb.4). Ihr Durchmesser beträgt ebenfalls maximal 100 μm.

Die Wand der lateralen Ovidukte besteht aus einer einfachen Lage von Ringmuskelfasern, die innen von einem einschichtigen Epithel ausgekleidet wird (Abb.7a). Dieses verdrängt mit seinen zahlreichen Falten das Lumen fast vollständig. Lichtmikroskopisch ließ sich weder eine Cuticulaauskleidung noch eine epitheliale Peritonealhülle nachweisen.

Eine chitinige Intima, wie sie Miller (1965) für die lateralen Ovidukte von *Drosophila melanogaster* beschreibt, scheint also bei *C. whitei* zu fehlen. TEM-Befunde liegen hierzu nicht vor.

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Abb.7: Ovidukte von *C. whitei*, Semidünnschnitte, Richardson. (a) Oviductus lateralis; im oberen Teil der Abbildung ist das proximale Ende des Ovars zu erkennen, das in den Oviductus lateralis übergeht,
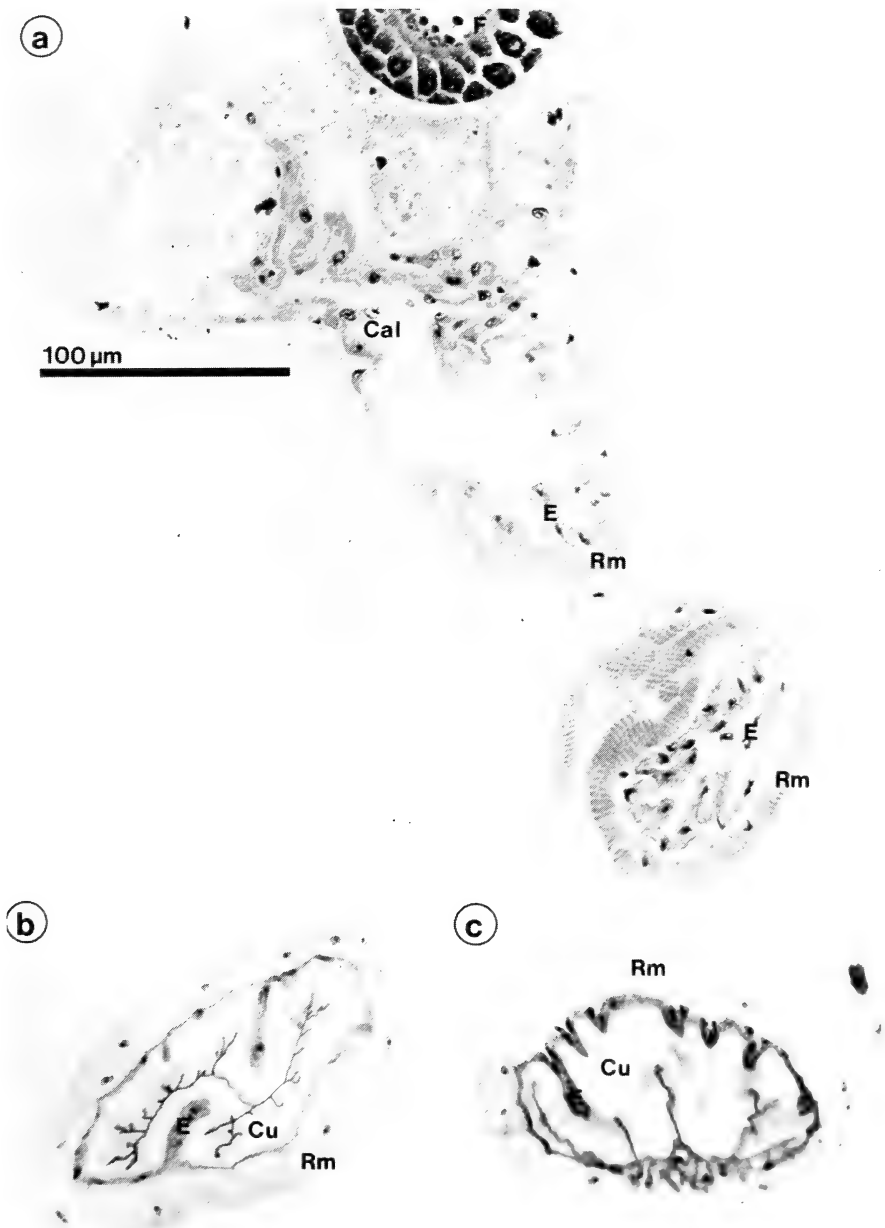
im unteren Teil ein Querschnitt des Oviductus lateralis; (b) Oviductus communis, cranialer Bereich;
(c) Oviductus communis, caudaler Bereich.

E: Epithel, F: Follikel, Cal: Calyx, Cu: Cuticula, Rm: Ringmuskulatur.

Oviductus communis

Der Oviductus communis ist ca. 800 μm lang und bildet in situ ventral vor dem cranialen Ende der Vagina eine kurze dorsoventrale Schlaufe (Abb.3b), bevor er in die Vagina einmündet. In entspanntem Zustand hat er einen ovalen Querschnitt von etwa 100x150 μm Durchmesser (Abb.7b,c).

Ein Knick im Oviductus communis wurde schon von Brüel (1897) bei *Calliphora erythrocephala* beschrieben. Wie bei *Calliphora* mag er auch bei *C. whitei* dazu nötig sein, daß die Vagina beim Ausstrecken des Abdomen zur Eiablage oder bei der Kopulation nach hinten verlagert werden kann, während die Ovarien in ihrer Position verbleiben. In Zusammenhang damit könnte der Knick die Stelle sein, an der ablagereife Eier zurückgehalten werden, bis durch Strecken der letzten Segmente (und somit des Oviduktes) die Eiablage eingeleitet wird (s. „Eiablage").

Die Wand des Oviductus communis besteht aus einer etwa 16 μm dicken Lage sich überlappender Ringmuskelfasern, die von einem einschichtigen Epithel ausgekleidet wird (Abb.7b,c). Ein peritonealer Überzug ist auch im TEM nicht nachweisbar. Das Epithel bildet durch Auffaltung zwei bis mehrere, in das Oviduktlumen vorspringende, longitudinale Falten, die bevorzugt nahe der dorsalen und ventralen Mittellinie verlaufen. Im TEM zeigen sich die Zellgrenzen zwischen den Epithelzellen stark gefaltet und fast vollständig durch septierte Desmosomen abgedichtet. Apikal tragen die Epithelzellen Mikrovilli. Die darüberliegende Cuticula verdrängt das verbleibende Lumen des Ovidukts fast vollständig. Ihre Mächtigkeit wird durch die teilweise sehr hohe Endocuticula bestimmt, die im TEM körnig und elektronenhell erscheint. Die elektronendichte Epicuticula ist nur ca. 0,1 μm dick.

Im Verlauf des Oviductus communis ändert sich die Ausprägung der Epithelfalten und die Dicke der Cuticula. Die Anzahl der Längsfalten nimmt caudad zu, ihre Höhe ab (Abb.7b,c). Im cranialen Teil ist die Dicke von Epithel (ca. 3 μm) und Cuticula (ca. 17 μm) ringsum gleichmäßig ausgebildet. Im caudal von der Knickstelle gelegenen Teil hingegen ist das Epithel der dorsalen Seite wesentlich dicker (ca. 6 μm) und enthält auffällig viele Mitochondrien. Darüberhinaus gewinnt die Endocuticula der dorsalen Seite so stark an Mächtigkeit (ca. 40 μm), daß sie fast den gesamten Ovidukt ausfüllt, während sie an der ventralen Seite kaum erkennbar ist. Schließlich ist dort, wo der Ovidukt das muskulöse Dach der Vagina durchdringt, die Cuticula sowohl ventral als auch dorsal insgesamt nur 0,15—0,20 μm dick (Abb.12A). Die Epithelzellen sind in diesem Bereich besonders stark miteinander verzahnt.

Bei einer Eipassage wird das Oviduktlumen sehr stark erweitert. Die Muskelwand wird gedehnt, die Epithelfalten werden gestreckt. Der Zusammenhalt der Epithelzellen ist durch stark gefaltete Zellkontakte mit septierten Desmosomen gesichert. Wie ein Vergleich des Epicuticulaumfanges (ca. 690 μm in Abb.7b) mit dem ebenfalls an Schnittpräparaten gemessenen Eiumfang (ca. 730 μm) zeigt, ist neben der Streckung der Cuticulafalten auch eine leichte Deformation des Eies während der Oviduktpassage nötig.

Durch ihre symmetrische Lage im Ovidukt können die Epithelfalten zur Orientierung des hindurchgleitenden Eies beitragen, dessen Unterseite in der Vagina stets ventral zu liegen kommt (s. „Eiablage"). Das Erscheinungsbild des Epithels im dorsalen caudalen Teil des Ovidukts scheint auf eine sekretorische Tätigkeit hinzuweisen, wie sie schon Brüel (1897) für den Ovidukt von *Calliphora erythrocephala* beschrieb.

Vagina

Die Vagina ist ein ca. 650 µm langer Muskelschlauch (Abb.4, 8). Ihr cranialer Teil hat einen Durchmesser von ca. 250 µm. In ihn münden dorsal der Oviductus communis und die Ausführgänge der Spermatheken und akzessorischen Drüsen, sowie ventral ein unpaares Receptaculum. Weiter caudal ist in die ventrale Vaginawand ein sklerotisierter Ring eingebettet. In diesem Bereich ist die Vagina etwa 200 µm breit, caudal vom sklerotisierten Ring wird sie zur Vulva hin noch schmäler.

Die hier verwendeten Bezeichnungen folgen Snodgrass (1935). Ihm zufolge liegt der primäre weibliche Gonoporus an der Einmündung des — selbst bereits ektodermalen — Oviductus communis in die von der Körperwand her invaginierte Genitalkammer. Die äußere Öffnung der Genitalkammer ist die Vulva. Die Genitalkammer ist nach Snodgrass als Vagina zu bezeichnen, wenn sie als tubuläre Fortsetzung des Oviductus communis ausgeprägt ist. Das in diesem Sinne als Vagina bezeichnete Organ von *C. whitei* kann nicht ohne weiteres mit gleichnamigen Organen in anderen Arbeiten über Dipteren homologisiert werden. Einige Autoren haben Teilbereiche der Genitalkammer mit gesonderten Bezeichnungen wie „Sacculus", „Uterus" u. ä. belegt und nur den Rest als Vagina bezeichnet (Diskussion 2.3).
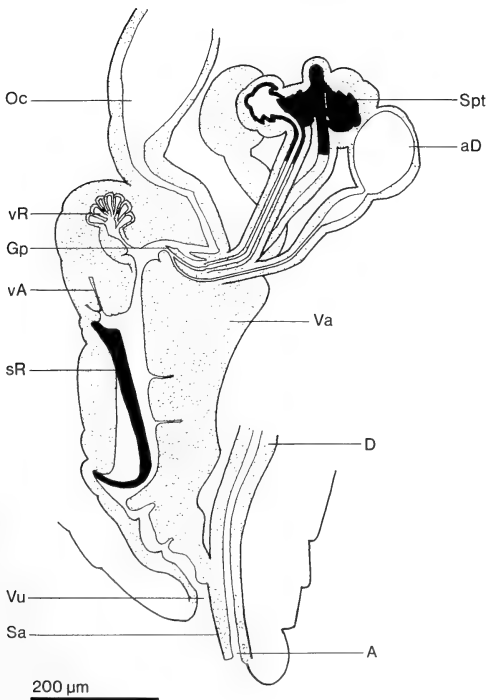
Abb.8: Innere weibliche Geschlechtsorgane von *C. whitei*, Lateralansicht von links, Ovarien und laterale Ovidukte nicht abgebildet.

A: Anus, aD: akzessorische Drüse, D: Darm, Gp: Genitalpapille, Oc: Oviductus communis, Sa: Subanalplatte, Spt: Spermathek, sR: sklerotisierter Ring, vA: ventrale Aussackung, Va: Vagina, vR: ventrales Receptaculum, Vu: Vulva.

Innere Organisation der Vagina

Dort, wo der Oviductus communis in den cranialen Teil der Vagina übergeht, ist der geradlinige Weg durch das in die ventrale Muskelwand der Vagina eingebettete ventrale Receptaculum versperrt (Abb.8, 10a). Das Lumen des Oviduktes verläuft innerhalb der dorsocranialen Muskelwand der Vagina nach dorsal und passiert dort als schmaler Spalt das Receptaculum, um sich vor der Genitalpapille wieder nach ventral zu wenden. Die Genitalpapille ist eine ca. 50 μm hohe Auffaltung der dorsalen Vaginawand (Abb.10a, b, 12F—K), in die von dorsal die Ausführgänge der Spermatheken und, etwas caudal davon, die der akzessorischen Drüsen münden.

Die Grenze zwischen Ovidukt und Vagina liegt nach Weidner (1982) an der Einmündung der Spermathekengänge, bei *C. whitei* also an der Genitalpapille. Es ist bei den höheren Dipteren verbreitet, daß die Ausführgänge von Spermatheken und akzessorischen Drüsen dicht hintereinander in einer Papille münden („genital papilla" bei *Glossina austeni* (Pollock 1974), „insemination pocket" bei *Dacus oleae* (Solinas & Nuzzaci 1984)). Sklerotisierungen im Mündungsbereich der Spermathekengänge, wie sie bei einigen Dipteren bekannt sind (Furca der orthorrhaphen Brachycera (McAlpine 1981), ringförmiger Sklerit bei *Sepsis punctum* (Kiontke 1989)), wurden bei *C. whitei* nicht gefunden.

Gegenüber der Genitalpapille liegt die von einem Epithelwulst umgebene Mündung des ventralen Receptaculum und etwas caudal davon eine unscheinbare weitere ventrale Aussackung, die keine besonderen Differenzierungen aufweist (Abb.8, 10a).

Da die caudal vom ventralen Receptaculum gelegene Aussackung der ventralen Vaginawand von *C. whitei* bei der Kopulation (s. „Kopulation") weder die männlichen Geschlechtsorgane noch das
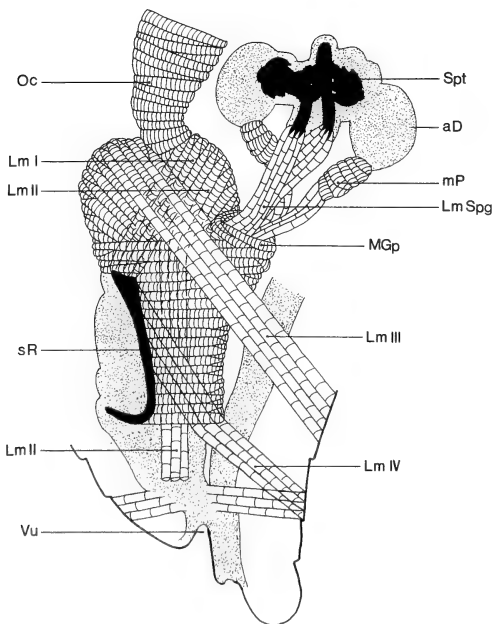
Abb.9: Muskulatur der inneren weiblichen Geschlechtsorgane von *C. whitei*, Lateralansicht von links.

aD: akzessorische Drüse, Lm I—IV: Längsmuskeln I—IV, LmSpg: Längsmuskulatur der Spermathekengänge, MGp: Muskeln an Genitalpapille, mP: muskulöse Pumpe, Oc: Oviductus communis, Spt: Spermathek, sR: sklerotisierter Ring, Vu: Vulva.

Ejakulat aufnimmt, ist sie nicht als Bursa copulatrix oder als Receptaculum einzuordnen. Diese Aussackung ermöglicht vielmehr die bei der Eiablage notwendige Volumenzunahme der Vagina (s. „Eiablage").

Von der Mündung des ventralen Receptaculum aus verläuft das Lumen der Vagina bis kurz vor der Vulva relativ geradlinig caudad (Abb.8). In der ventralen Wand der Vagina bildet die Cuticula einen stark sklerotisierten, längsovalen Ring aus (Abb.3b, 8, 9, 11b, c, 12L—O), dessen caudales Ende ventrad umgebogen ist. Der Ring ist ca. 10 μm stark und spannt eine ca. 250 μm lange und 100 μm breite, glatte Cuticulafläche aus, unter der ein Polster aus besonders differenzierten Epithelzellen liegt (s. u.).

Derartige Ringstrukturen sind schon für Diopsiden der Gattungen *Diopsis* und *Diasemopsis* (van Bruggen 1961, Tan 1965) abgebildet worden. Auch in einigen anderen Dipterenfamilien wurden ringförmige Sklerite in der ventralen Wand der Genitalkammer beschrieben, beispielsweise bei Phoridae (Brown 1988) und Canacidae (Wirth 1989). Eine Homologie dieser Strukturen wäre denkbar, bleibt jedoch zu überprüfen (Diskussion 2.3).

Obwohl ein Teil des sklerotisierten Ringes von *C. whitei* beim Hervorstülpen der Vagina bei der Kopulation (s. dort) an der Körperoberfläche hinter dem Sternit 8 zu liegen kommt, ist er nicht dem Sternit 9 homolog. Da sich die Vulva vor dem Sternit 9 befindet, kann dieses bei einer Verlagerung nach innen nur in der dorsalen Wand der Vagina zu liegen kommen, wie es bei der auf diesem Wege entstandenen Furca vieler Nematocera und orthorrhapher Brachycera der Fall ist (McAlpine 1981).

Gegenüber vom sklerotisierten Ring wird das Vaginalumen durch vornehmlich longitudinale Epithelfalten bis auf einen schmalen Spalt eingeengt (Abb.12M—O). Eine besonders voluminöse Epithelfalte beginnt dorsal nahe der Genitalpapille als breites, medianes Polster und zieht, schmäler werdend und durch seitliche Einschnürungen strukturiert, caudad bis zur Vulva. Caudal vom umgebogenen Ende der sklerotisierten Ringstruktur nimmt der Durchmesser der Vagina weiter ab (Abb.8). Dieses letzte Stück der Vagina wird von kleineren longitudinalen und transversalen Falten eingeengt.

Muskulatur der Vagina

Eine dicke, mehrschichtige Ringmuskulatur (Rm) umgibt die Vagina von deren cranialem Ende bis zum caudalen Ende des sklerotisierten Ringes (Abb.9, 10c, 12B—N, 43b). Die den dorsocranialen Bereich der Vagina überspannenden transversalen Muskelfasern (Tm) (Abb.12A) gehen seitlich in Längsmuskeln (Lm I + II) über (Abb.12B), die innerhalb der Ringmuskelschicht caudad ziehen. Ein Teil von ihnen (Lm I) inseriert am cranialen Ende des sklerotisierten Ringes, während der Rest (Lm II) bis zum Hinterrand der Vulva reicht. Ein Muskelpaar (Lm III) entspringt seitlich im cranialen Bereich der Vagina und zieht caudolateral zum Tergum 7. Einige seiner Fasern kommen aus dem ventralen Teil der Ringmuskulatur, andere setzen dorsolateral an den Cuticulakammern des ventralen Receptaculum an (Abb.12C—E, 14a). Im Bereich des sklerotisierten Ringes umspannt die Ringmuskulatur nicht die gesamte Vagina, sondern setzt an dem sklerotisierten Ring an und zieht von dort aus um die Vagina herum nach dorsal, wo die Muskelfasern ineinandergreifen (Abb.12L—N). Vom sklerotisierten Ring ziehen außerdem zwei seitliche Muskelbündel (Lm IV) innerhalb der Ringmuskulatur dorsocaudad zur Hinterkante des Tergum 8. Caudal vom sklerotisierten Ring ziehen Muskelfasern

von der ventralen Seite der Vagina zum Sternum 8 und von der dorsalen Seite der Vagina zum Hinterrand des Tergum 8.
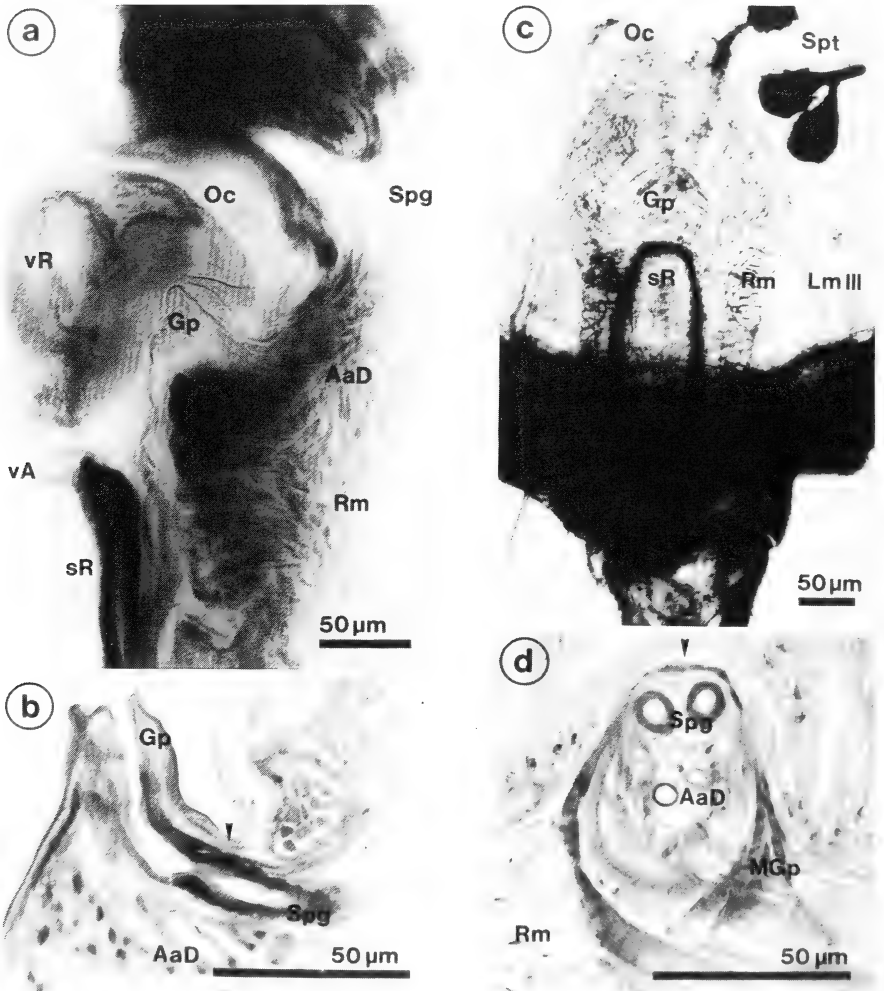
Abb.10: Vagina von *C. whitei*, Genitalpapille. (a) Lateralansicht von links, Totalpräparat, Toluidinblau; (b) medianer Semidünnschnitt (während der Besamung fixiert, vergl. Abb.44), Richardson; (c) Dorsalansicht, Totalpräparat, ungefärbt; (d) frontaler Semidünnschnitt, Richardson.

AaD: Ausführgänge der akzessorischen Drüsen, Gp: Genitalpapille, Lm III: Längsmuskel zum Tergum 7, MGp: Muskeln an Genitalpapille, Oc: Oviductus communis, Rm: Ringmuskulatur, Spg: Spermathekengänge, Spt: Spermatheken, sR: sklerotisierter Ring, vA: ventrale Aussackung, vR: ventrales Receptaculum, Pfeil: verdickte Cuticulaplatte über der Mündung der Spermathekengänge.

Die Muskulatur der Vagina von *C. whitei* ist weitgehend mit der von *Drosophila melanogaster* (Miller 1965) und *Calliphora erythrocephala* (Brüel 1897) vergleichbar. Bei *C. whitei* konnte jedoch keine muskulöse Verbindung zwischen dem dorsocranialen Teil der Vagina und dem Darm gefunden werden, wie sie bei *Calliphora* beschrieben ist. Der ventrale sklerotisierte Ring, dem bei *C. whitei* eine wesentliche Bedeutung als Muskelansatzstelle zukommt, fehlt *Drosophila* und *Calliphora*. Dementsprechend umgreift dort die Ringmuskulatur die gesamte Vagina („Uterus"), während bei
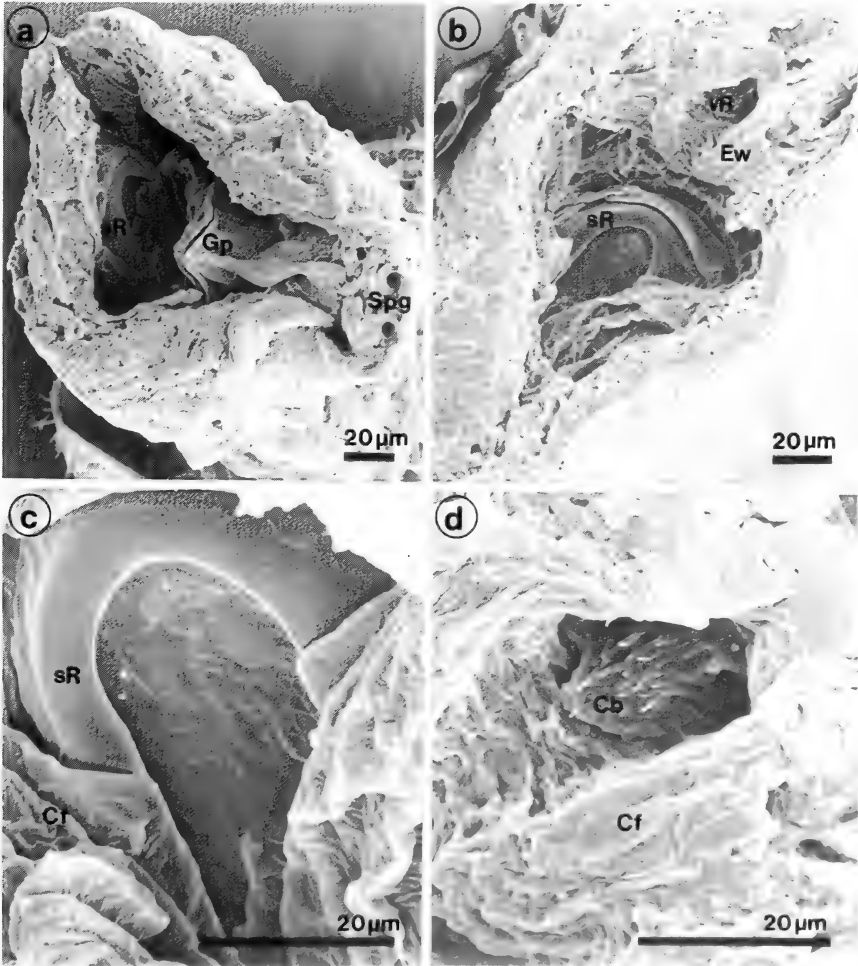
Abb.11: Vagina von *C. whitei*, REM. (a) Blick von cranial in eine aufgeschnittene Vagina; (b) Blick von dorsal in eine aufgeschnittene Vagina; (c) sklerotisierter Ring, stärkere Vergrößerung von (b); (d) Mündung des ventralen Receptaculum, stärkere Vergrößerung von (b).

Cb: Cuticulaborsten, Cf: Cuticulafalten, Ew: Epithelwulst, Gp: Genitalpapille, Spg: Spermatheken-gänge, sR: sklerotisierter Ring, vR: Mündung des ventralen Receptaculum.

C. whitei das vom sklerotisierten Ring eingefaßte Epithelpolster von der Muskulatur ausgespart bleibt (s.u.).

Epithel der Vagina

Die Vagina ist von einer (mit Ausnahme des sklerotisierten Ringes) nicht sklerotisierten, stellenweise bis zu 50 μm dicken Cuticula ausgekleidet, die einem einschichtigen Epithel aufliegt. Epithel und Cuticula bilden zahlreiche große und kleinere Falten (Abb.11, 12).

Eine besondere Differenzierung weist das von der sklerotisierten Ringstruktur eingegrenzte Epithel auf, welches ein bis zu 60 μm dickes, einschichtiges Polster bildet (Abb.12M, 13). Die großen Kerne liegen basal, zwischen einem Labyrinth aus Lymphlakunen. Die Basis der Epithelzellen und die Öffnungen der Lymphlakunen sind nur durch eine ca. 0,1 μm dicke Basallamina vom Hämolymphraum getrennt. Apikale Cytoplasmamembranfalten der Epithelzellen bilden auffällige Membranstapel, die an der cytoplasmatischen Seite mit elektronendichten Partikeln von ca. 9 nm Durchmesser besetzt sind (Abb.13b). Zwischen den Membranen liegen zahlreiche Mitochondrien. Die Cuticula über diesen Epithelzellen weist zwei Schichten auf. Die dickere, basale Schicht ist relativ elektronenhell und besitzt eine körnige Struktur. Die apikale Cuticulaschicht ist elektronendichter und nur etwa 0,8 μm dick. Poren konnten in der Cuticula nicht identifiziert werden.
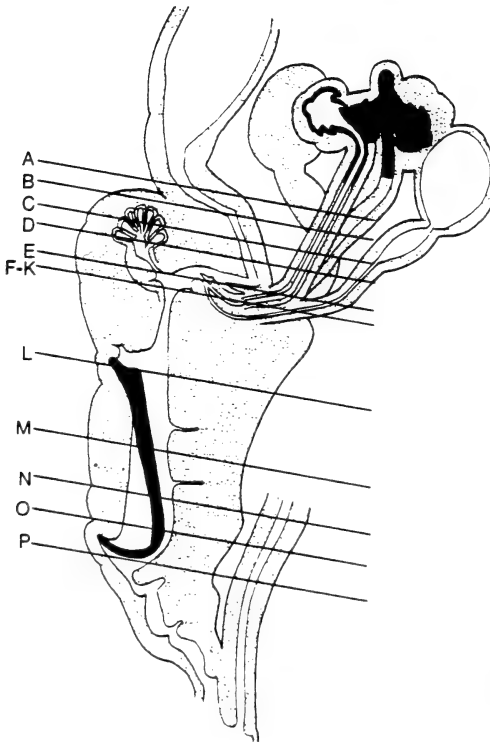
Abb.12: Vagina von *C. whitei*, Semidünnschnittserie, quer, von cranial nach caudal, Richardson. Die Schnittebenen sind nebenstehender Zeichnung zu entnehmen. Vergrößerung stets gleich. Jedes Merkmal ist nur in einer Abbildung beschriftet.

AaD: Ausführgang einer akzessorischen Drüse, Cb: Cuticulaborsten, Cu: Cuticula, D: Darm, Dp: Epithelpolster, E: Epithel, Ew: Epithelwulst, Gp: Genitalpapille, Lm I—III: Längsmuskeln I—III, MaD: Mündung der akzessorischen Drüsen, MSpg: Mündung der Spermathekengänge, MvR: Mündung des ventralen Receptaculum, Oc: Oviductus communis, Rm: Ringmuskulatur, Spg: Spermathekengänge, sR: sklerotisierter Ring, Tm: transversale Muskelfasern, Va: Vaginalumen, vR: ventrales Receptaculum.
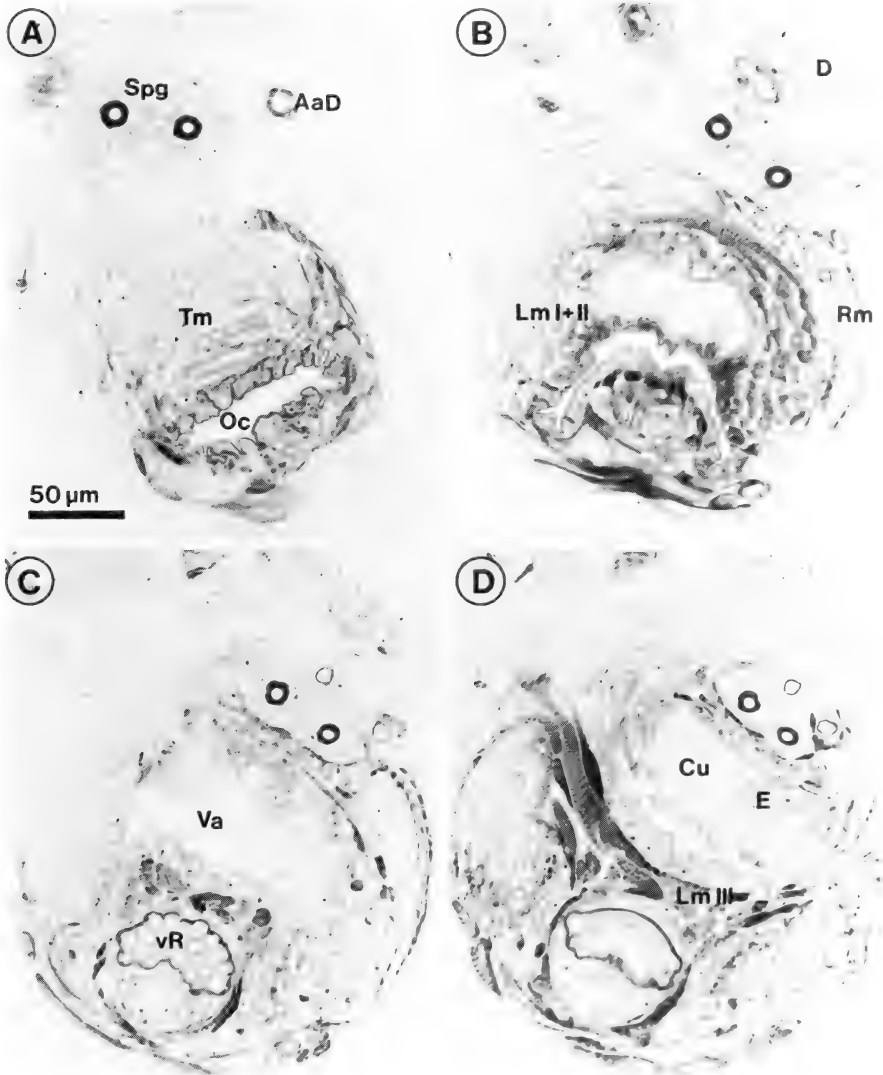
Abb.12A—D: Erläuterungen siehe Abb.12
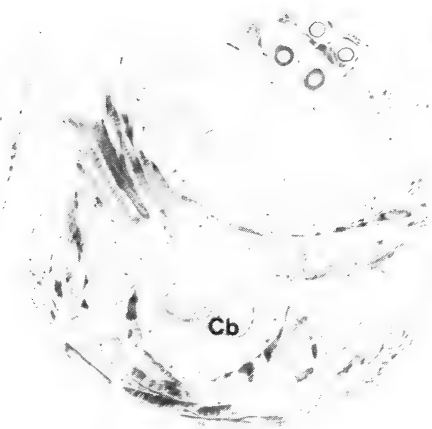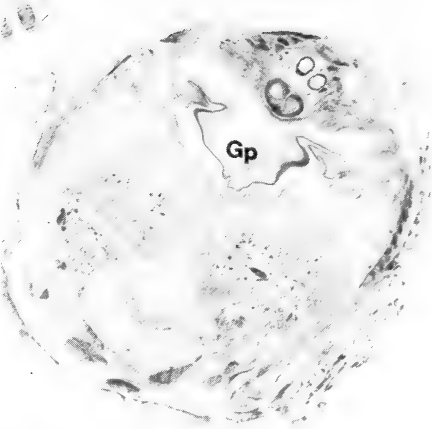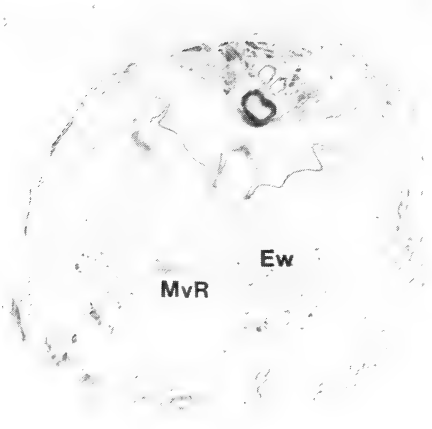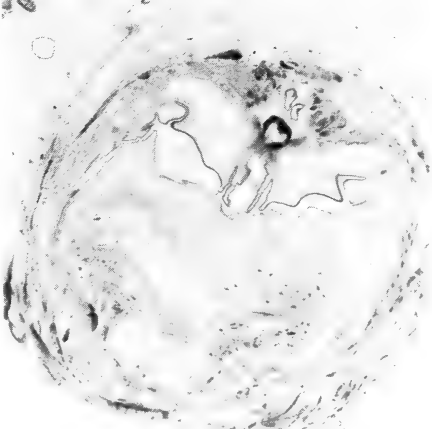
Abb.12E—H: Erläuterungen siehe Abb.12
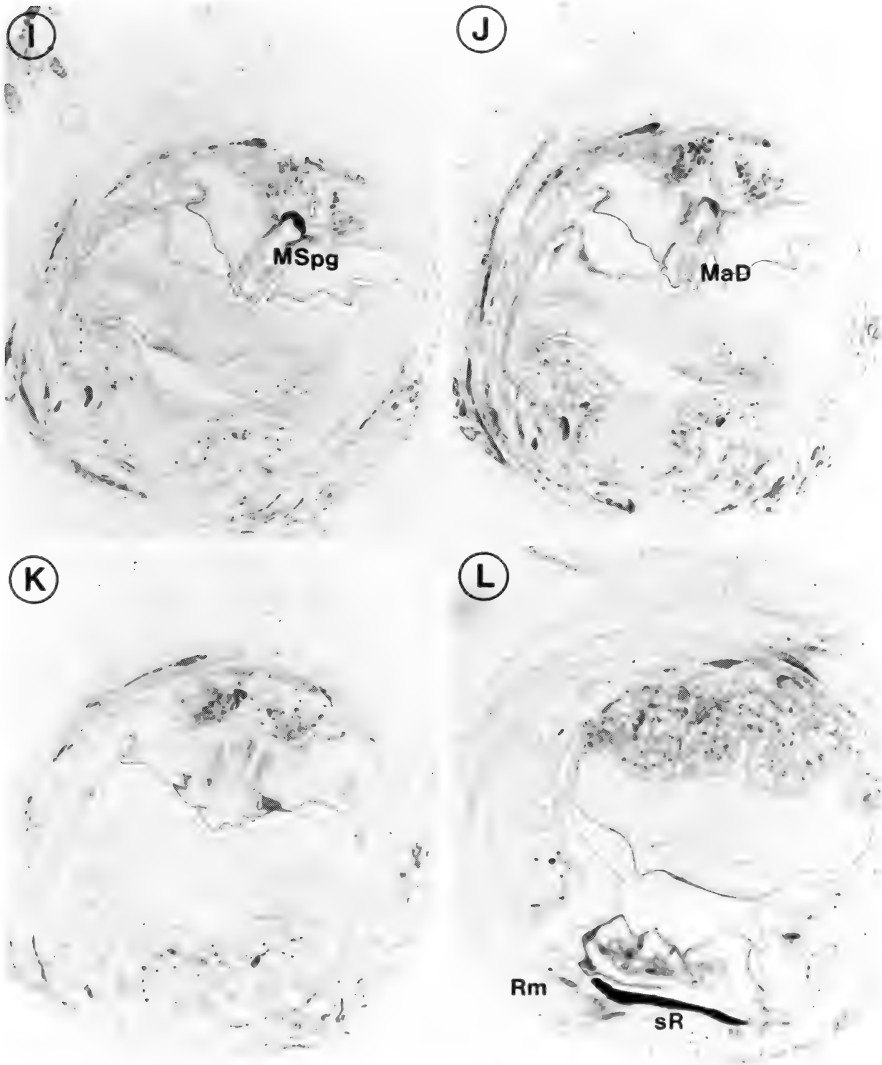
Abb.12I—L: Erläuterungen siehe Abb.12
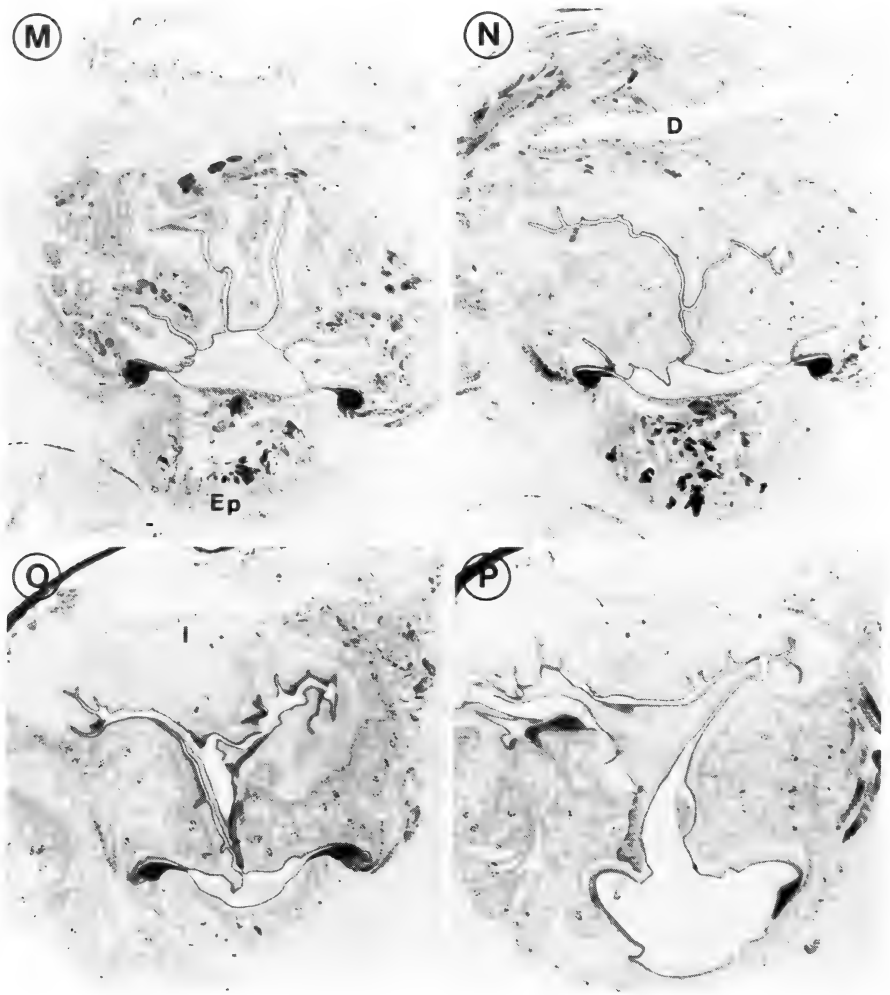
Abb.12M—P: Erläuterungen siehe Abb.12

Abb.13: Vom sklerotisierten Ring eingefaßtes Epithelpolster in der ventralen Wand der Vagina von *C. whitei* (vergl. Abb.12M—O), TEM. (a) apikaler Teil der Epithelzellen mit darüberliegender Cuticula; (b) Membranstapel, Sterne markieren die mit elektronendichten Partikeln besetzte cytoplasmatische Seite der Membranen; (c) basaler Teil des Epithels.
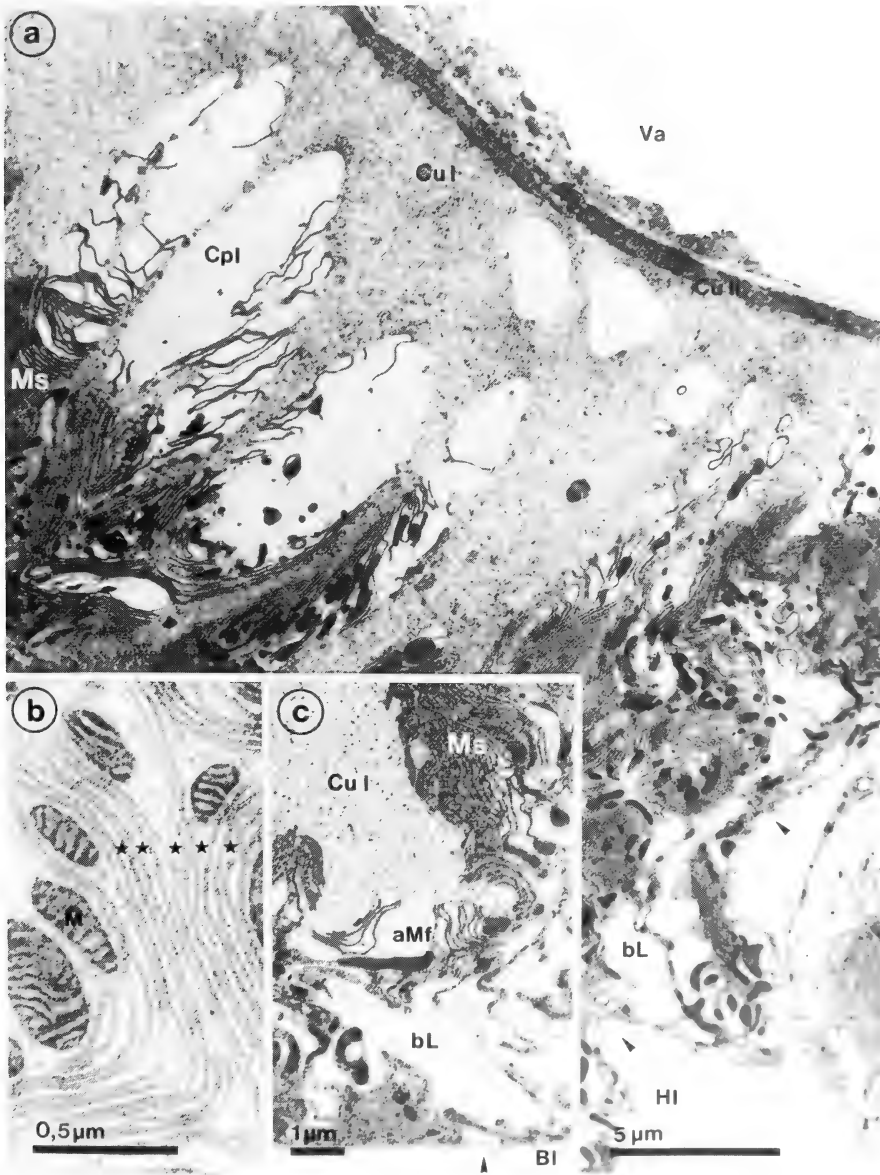
aMf: apikale Cytoplasmamembranfalten, bL: basales Labyrinth, Bl: Basallamina, Cpl: Cytoplasmalaku-
nen, Cu I: basaler Teil der Cuticula, Cu II: apikaler Teil der Cuticula, Hl: Hämolymphraum, M: Mito-
chondrium, Ms: Membranstapel, Va: Vaginalumen, Pfeile: basale Öffnungen des Lymphlakunensystems.

Das basale Lymphlakunensystem und die apikalen, partikelbesetzten Membranstapel, zwischen denen zahlreiche Mitochondrien liegen, lassen vermuten, daß an diesen Strukturen ein Ionen- und/oder Wassertransport stattfindet (siehe auch „Spermatheken"). Möglicherweise steht die Entwicklung des sklerotisierten Ringes mit der Funktion dieses Epithels in Zusammenhang. Indem die Muskulatur an diesem Ring ansetzt, bleibt das Epithelpolster in seiner Mitte von Muskulatur ausgespart, was den Diffusionsweg zwischen Epithel und Hämolymphe wesentlich verringert. Außerdem sind auf diese Weise die Zellen des Epithelpolsters und die darüberliegende Cuticula von einer Kraftübertragung seitens der Ringmuskulatur der Vagina weitgehend abgekoppelt.

Ventrales Receptaculum

Am cranialen Ende der Vagina liegt, eingebettet in deren ventrale Muskelwand, das ventrale Receptaculum (Abb.8, 10a, 12C—F). Es besteht aus einem kurzen Gang, in den distal 30—40 kegelförmige Cuticulakammern einmünden (Abb.14). Ihre gefächerte Anordnung erinnert an eine halbierte Himbeere. Die ventrale Wand des Ganges trägt ein Cuticulaborstenfeld. Bei der Eiablage werden die Eier an der Öffnung des ventralen Receptaculum mit in den Cuticulakammern gespeicherten Spermatozoen besamt.

Ein ventrales Receptaculum ist bereits bei vielen acalyptraten Schizophora bekannt (Tab.2), war bei den Diopsiden jedoch bisher noch nicht beschrieben. Die Bezeichnung als „ventrales Receptaculum" ist bei C. whitei aufgrund der Lage des Organs und seiner Funktion als Spermatozoenspeicher gerechtfertigt. Sie soll vorerst mit keiner Aussage über eine Homologie mit den gleichnamigen Organen anderer Dipteren verbunden sein. Dem ventralen Receptaculum von C. whitei in Lage, Struktur und Funktion sehr ähnliche Organe sind bereits bei Tephritidae und Otitidae beschrieben und unterschiedlich benannt worden (Diskussion 2.2).

Im Bereich der Cuticulakammern hat das ventrale Receptaculum mit bis zu 60 μm seinen größten Durchmesser (Abb.14b, c). Das komplizierte Gebilde besteht gänzlich aus nicht sklerotisierter Cuticula. Die kegelförmigen Kammern haben distal einen Durchmesser von 6,7—7,5 μm und einen runden Querschnitt. Proximal ist ihr Querschnitt mehr oder weniger sternförmig eingeengt. Die Länge der Kammern beträgt ca. 15 μm.

Die terminale Wand der Cuticulakammern ist ca. 2,5 μm dick und zeigt im TEM eine auffällige Schichtung (Abb.16). Die basale Schicht I besteht aus relativ homogenem Material. Sie bildet unregelmäßige Fortsätze aus, die in das umgebende Epithel hineinragen. Zum Kammerlumen hin schließt sich eine quer zur Oberfläche parallelfaserig strukturierte Schicht II an. Schließlich folgt eine relativ elektronendichte Schicht III, welche die Kammern terminal wie ein Deckel abschließt und seitlich mit Schicht I in Kontakt steht. Die Trennwände zwischen den Kammern enthalten sowohl homogenere als auch faserig strukturierte Cuticulabereiche. Apikal laufen sie in lange Cuticuladornen aus (Abb.14a,b,d).

Überlegungen zur möglichen Funktion der gekammerten Struktur des ventralen Receptaculum finden sich in der Diskussion (1.2).

Abb.14: Ventrales Receptaculum von C. whitei, Semidünnschnitte, Richardson. (a) median; (b) frontal; (c—e) Querschnitte in verschiedenen Höhen (siehe (b)). Vergrößerung stets gleich.
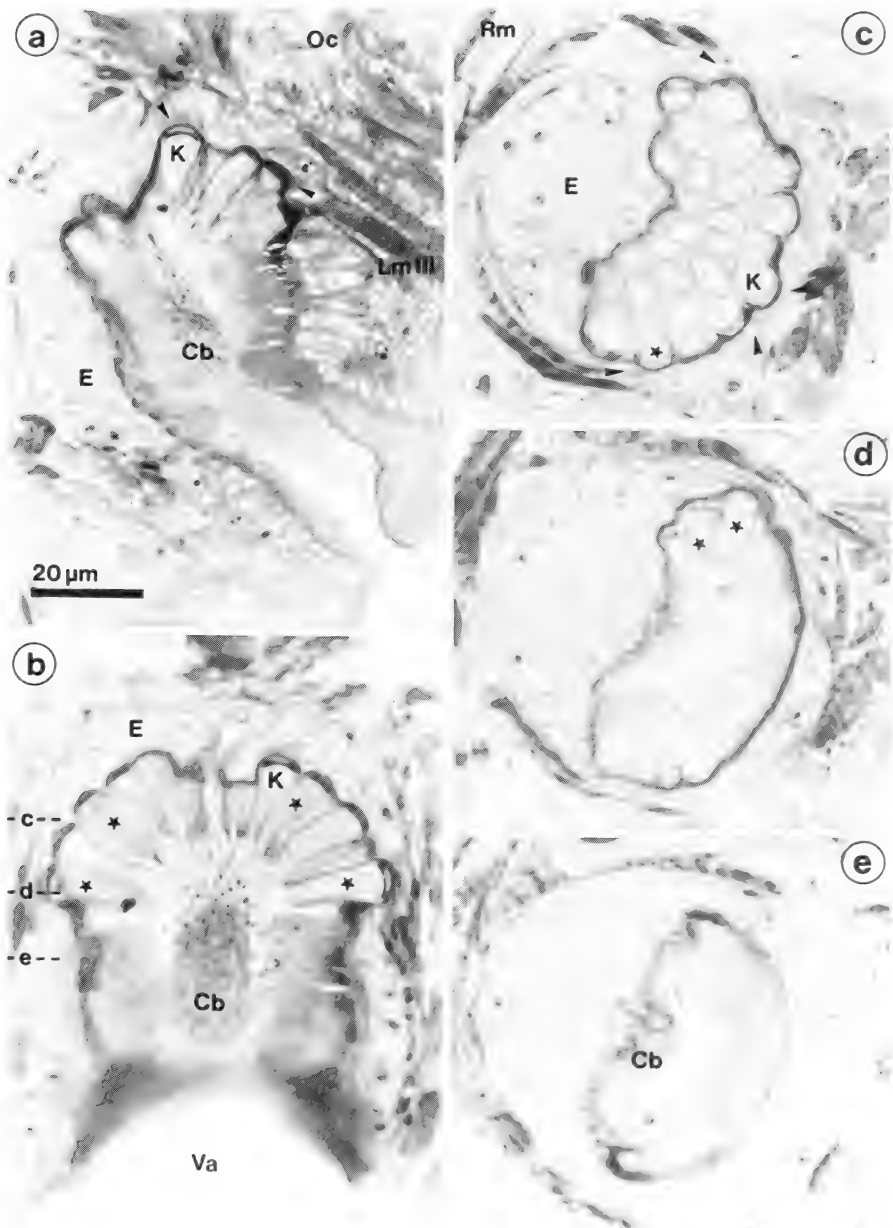
Cb: Cuticulaborsten, E: Epithel, K: Cuticulakammern, Lm III: Längsmuskel III, Oc: Oviductus commu-
nis, Rm: Ringmuskulatur, Va: Vaginalumen, Pfeile: Muskelansatzstellen an den Cuticulakammern.
Sterne markieren Cuticulakammern, die aufgerollte Spermatozoen enthalten.

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Der zuführende Gang ist ca. 50 μm lang und ca. 20 μm weit. Rings um das Lumen sind Cuticulaborsten ausgebildet, die zur Vagina hin weisen (Abb.11d, 14, 15). An der ventralen Wand stehen diese Borsten besonders dicht und sind teilweise zu einem erhöhten Polster verschmolzen, welches das Lumen des Ganges stark einengt. Die Cuticulaborsten sind nicht innerviert (s. „Innervierung").

Da den Cuticulaborsten im zuführenden Gang wegen der fehlenden Innervierung keine sensorische Funktion zukommen kann, muß ihre Funktion eine mechanische sein. Hierfür sind mehrere Möglichkeiten denkbar. Die Borsten könnten den Eingang zum ventralen Receptaculum versperren, und so einen unbeabsichtigten Spermatozoenverlust aus den Cuticulakammern (Solinas & Nuzzaci 1984) oder ein unerwünschtes Eindringen von Spermatozoen aus der Vagina verhindern. Andererseits könnten sie eindringenden Spermatozoen aber auch als Orientierungshilfe dienen oder ihnen ein strukturiertes Substrat bieten, als Voraussetzung für eine gerichtete Vorwärtsbewegung (s. „Spermatozoen"). Das Borstenfeld nimmt möglicherweise das Sekret der akzessorischen Drüsen wie ein Pinsel auf, um es bei der Eiablage (s. dort) auf den die Mikropyle bedeckenden Sekretpfropf zu übertragen. Ein ähnlicher Sachverhalt ist bei *Musca domestica* nachgewiesen (Leopold & Degrugillier 1978), wo das Sekret der akzessorischen Drüsen zusammen mit der mechanischen Wirkung der Cuticulaborsten in der Befruchtungskammer die Auflösung der Sekretkappe bewirkt.
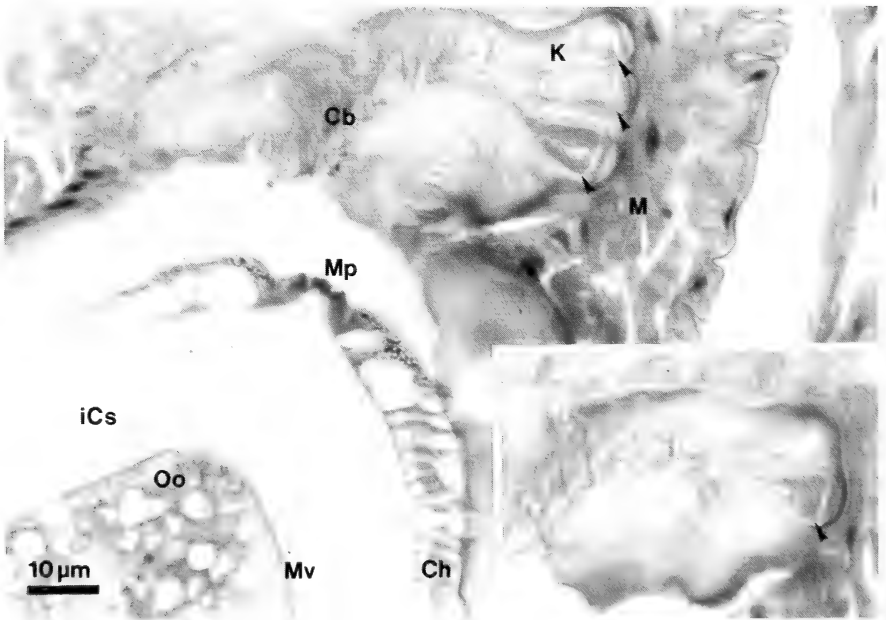
Abb.15: Ventrales Receptaculum von *C. whitei*, während der Besamung fixiert, medianer Semidünnschnitt (vgl. Abb.44), Richardson; Einsatz: weiterer Schnitt derselben Serie.
Cb: Cuticulaborsten, Ch: Chorion, iCs: innerste Chorionschicht, K: Cuticulakammern, Mp: Mikropyle, Mv: Membrana vitellina, Oo: Ooplasma, Pfeile: Spermatozoen in den Cuticulakammern. Der Hohlraum zwischen Eischale und Membrana vitellina ist ein Schrumpfungsartefakt.
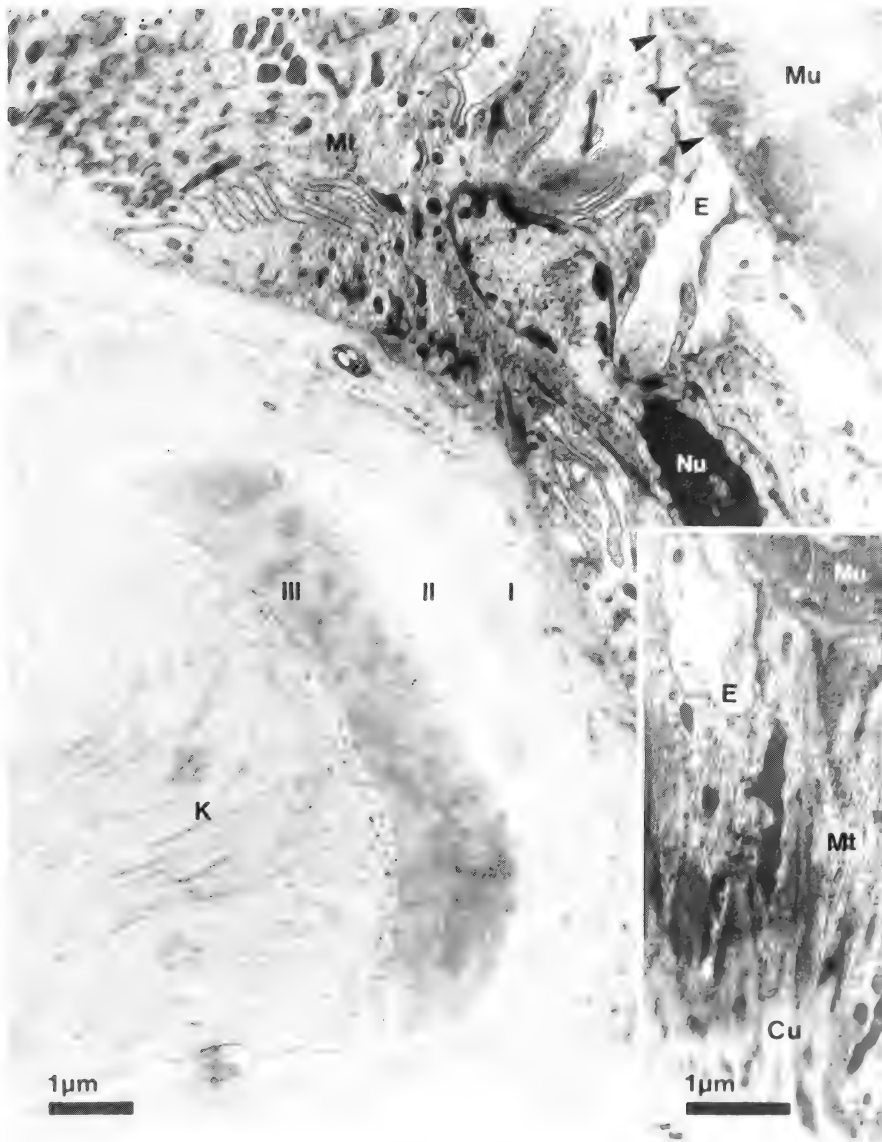
Abb.16: Ventrales Receptaculum von *C. whitei*, distales Ende einer Cuticulakammer, TEM; Einsatz: Mikrotubulibündel durchziehen die Epithelzellen von den Cuticulafortsätzen des Receptaculum bis zu den Muskelansatzstellen.

Cu: Cuticula, E: Epithel, K: Cuticulakammer, Mt: Mikrotubuli, Mu: Muskel, Nu: Nucleus, I—III: Cuticulaschichten I—III, Pfeile: Muskelansatzstellen.

Das ventrale Receptaculum ist von einem kubischen Epithel mit vorwiegend basal angeordneten Zellkernen umgeben (Abb.14). Zahlreiche Mikrotubuli inserieren bündelweise an den Fortsätzen der Cuticulaschicht I (Abb.16) und ziehen von dort zur Basis des Epithels, wo im lateralen und dorsalen Bereich des Receptaculum Muskelfasern inserieren (Abb.12 B—E, 14, 16). Von den lateralen Cuticulakammern ziehen Muskelfasern um das Receptaculum herum nach ventral, wo sie sich überkreuzen, um dann in die Ringmuskulatur (Rm) überzugehen. Außerdem zieht ein Muskelpaar (Lm III) von den dorsalen Kammern des Receptaculum nach dorsolateral zum Tergum 7. Abgesehen von den Muskeln, die am Receptaculum selbst inserieren, ist dieses auch noch von der Muskulatur der ventralen Vaginawand umgeben.

Nach McAlpine (1981) besitzt das ventrale Receptaculum der acalyptraten Schizophora nie eine eigene Muskulatur. Das ventrale Receptaculum von *C. whitei* weicht in diesem Punkt von der Definition ab. Die Assoziation der Cuticulafortsätze über die Mikrotubulibündel in den Epithelzellen mit den basal inserierenden Muskelfasern weist darauf hin, daß hier eine Kraftübertragung stattfindet.

Die dorsolateralen Muskelbänder (Lm III) ziehen das Receptaculum nach dorsal und caudal, und erweitern es dabei wahrscheinlich auch. Sie treten in verschiedenen Phasen der Eiablage in Aktion und spielen möglicherweise auch beim Spermatransfer aus den Spermathekengängen ins ventrale Receptaculum eine Rolle (s. „Eiablage"). Die Muskelfasern, die seitlich von den Cuticulakammern nach ventral ziehen und sich dort überkreuzen, können eine Verformung des Receptaculum bewirken, wobei möglicherweise der Inhalt der Cuticulakammern ausgepreßt wird. Wie sich die aus unterschiedlich strukturierten Schichten aufgebauten Kammerwände unter der Zugkraft der schräg ansetzenden Muskelfasern verhalten, muß noch untersucht werden.

Das ventrale Receptaculum unbegatteter Weibchen enthält eine filamentöse Substanz, die im TEM dem Inhalt der Spermatheken und Spermathekengänge gleicht (Abb.16). In Nativpräparaten von begatteten Weibchen können in den Cuticulakammern des ventralen Receptaculum aufgerollte, bewegliche Spermatozoen (s. dort) beobachtet werden, die zu rotieren scheinen. Die Kammern enthalten in der Regel nur ein bis zwei Spermatozoen (Abb.14a,c,d). Bei Weibchen, die während der Eiablage fixiert wurden, sind hingegen etliche Spermatozoen pro Kammer vorhanden (Abb.15).

Spermatheken

Die Spermatheken von *C. whitei* sind stark sklerotisiert und schon makroskopisch als dunkelbraune, dornige Körperchen sichtbar. Es sind 3 Spermatheken ausgebildet, von denen die beiden rechten einen gemeinsamen Ausführgang haben, während die linke einen eigenen Ausführgang besitzt (Abb.8, 17). Die beiden Spermathekengänge vereinigen sich kurz vor ihrer Einmündung in die Genitalpapille. Während die Spermatheken selbst mit keinerlei Muskulatur und Innervierung versehen sind, besitzen ihre Ausführgänge eine reich innervierte Längsmuskulatur. Neben der Funktion als Speicherorgan für Spermatozoen muß den Spermatheken nach histologischen Befunden auch eine sekretorische Tätigkeit zugeschrieben werden.
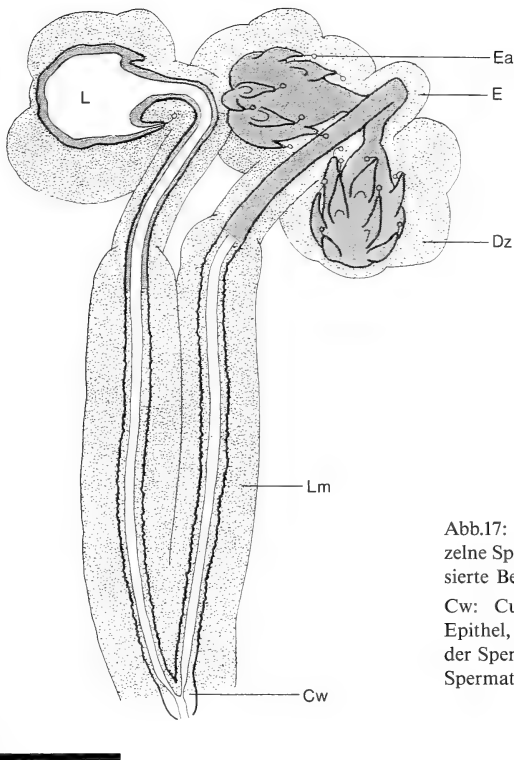
Abb.17: Spermatheken von *C. whitei*, einzelne Spermathek im Längsschnitt, sklerotisierte Bereiche dunkelgrau.

Cw: Cuticulawulst, Dz: Drüsenzelle, E: Epithel, Ea: Drüsenendapparat, L: Lumen der Spermathek, Lm: Längsmuskulatur der Spermathekengänge.

100 µm

Asymmetrie der Spermatheken

Bei den insgesamt etwa 1000 präparierten Weibchen wurden ohne Ausnahme 3 Spermatheken gefunden. In der Regel ist das distale Ende der Spermathekengänge mitsamt den Spermatheken mehr oder weniger weit nach proximal umgebogen, beide Gänge sind etwas nach rechts geneigt, und der rechte trägt das Spermathekenpaar. Der Darm führt in diesem Fall links an den Spermatheken vorbei. Nur bei drei von 220 auf diese Asymmetrie hin untersuchten Weibchen waren die Spermathekengänge nach links geneigt, während der Darm rechts vorbei lief; einmal trug der linke Gang das Spermathekenpaar.

Drei Spermatheken an zwei Gängen sind bei den acalyptraten Schizophora weit verbreitet (McAlpine 1989) und nach Feijen (1989) bei Diopsiden die Regel, von der allerdings in mehreren Gattungen abgewichen wird (Diskussion 2.1). Eine innerartliche Variabilität der Spermathekenzahl, wie sie bei *Drosophila melanogaster* (2—3 Spermatheken (Miller 1965, Shorrocks 1972)) beschrieben ist, wurde bei *C. whitei* nicht gefunden. Das gleiche gilt für die bei *C. whitei* fast immer gleichsinnige Asymmetrie.

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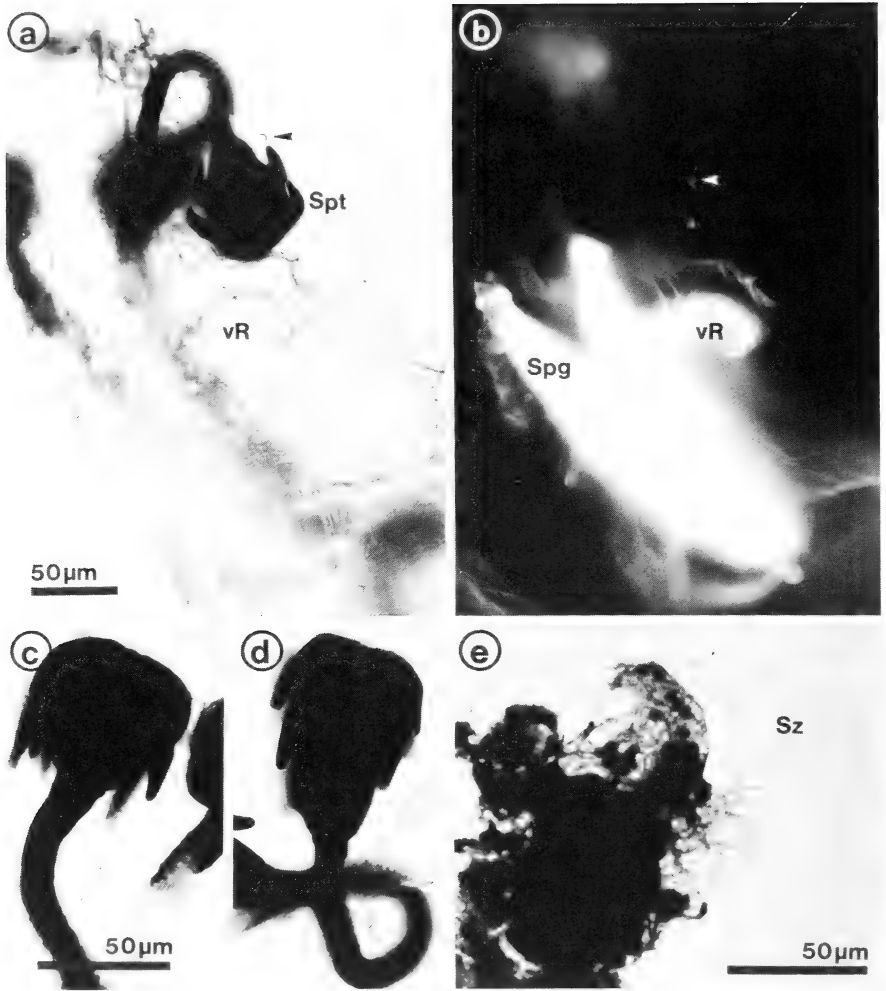
Abb.18: Spermatheken von *C. whitei*. (a) Totalpräparat, etwas mazeriert; (b) dasselbe Präparat unter UV-Anregung; (c—d) Nativpräparate, Spermathekenform rund bis birnenförmig; (e) Quetschpräparat, Hämatoxilin-Fuchsin.

Spg: Spermathekengänge, Spt: Spermathek, Sz: Spermatozoen, vR: ventrales Receptaculum, Pfeil: Drüsenendapparat.

Morphologie der Spermatheken

Die Spermatheken haben eine runde bis birnenförmige Gestalt, bei einem Durchmesser von ca. 45—50 μm und einer Höhe von ca. 60 μm (Abb.17, 18a,c,d). Proximal verjüngen sie sich fast übergangslos zum Spermathekengang. Jede Spermathek trägt etwa 10—12 nach proximal weisende Dornen, deren Form an Eiszapfen erinnert. Das Lumen der

Spermatheken setzt sich in diese Dornen hinein fort. An der Spitze jedes Dorns hängt ein feiner cuticulärer Gang, der an seinem Ende ein kleines Cuticulabläschen trägt (Abb.18a,b, 19f).

Feijen (1986) hat diese Cuticulabläschen bei verschiedenen Diopsiden dargestellt und als „tiny satellites, linked with fine filaments to the main body" beschrieben. Es handelt sich um die Endapparate von Kanaldrüsenzellen (s.u.). Leydig beschrieb schon 1867 einzellige Drüsen mit cuticulären Ausführgängen an den Spermatheken von *Tachina fera*. Seitdem sind sie bei etlichen Dipteren beschrieben, an der Spermathekenkapsel oder am -gang, in Gruppen gelagert oder verstreut (Clements & Potter 1967, Jordan 1972, Filosi & Perotti 1975, Solinas & Nuzzaci 1984 und andere). Wahrscheinlich sind die Spermatheken aller Dipteren mit derartigen Drüsenzellen versehen, wenn auch die Endapparate leicht bei der Präparation verloren gehen oder übersehen werden können.

Bedornte Spermatheken wurden in verschiedenen Dipterenfamilien beschrieben (Anthomyiidae (Wesché 1906), Nettiophilidae (Hennig 1958), Tephritidae (Hardy 1980), Anthomyzidae (Hardy 1980)). Bei *C. whitei* und einigen anderen Diopsiden und auch bei einigen Tephritiden und Micropeziden stehen die cuticulären Ausführkanäle der Drüsenendapparate mit den Spitzen der hohlen Spermathekendornen in Verbindung (eigene Untersuchungen), was auf einen funktionellen Zusammenhang hinweisen könnte. Allerdings sind auch glatte Spermatheken mit Drüsenzellen bestückt.

Walker (1980) nimmt an, daß die Form der Spermatheken mit der Paarungsstrategie bzw. dem Ausmaß der Spermaverdrängung oder -verdünnung bei aufeinanderfolgenden Kopulationen zusammenhängt. Ihm zufolge sollten rundliche Spermatheken wie die von *C. whitei* eher mit Monogamie oder einem höheren Fortpflanzungserfolg des jeweils ersten Kopulationspartners verbunden sein, tubuläre Spermatheken hingegen eher mit Polygamie und einem höheren Fortpflanzungserfolg des letzten Männchens.

Die Wand der Spermatheken besteht aus einer etwa 2 μm hohen geschichteten Cuticula. Infolge starker Sklerotisierung erscheint sie braun bis schwarz und zeigt, im Gegensatz zur nicht sklerotisierten Cuticula des restlichen Reproduktionstraktes, unter UV-Anregung keine Fluoreszenz (Abb.18b).

Eine starke Sklerotisierung der Spermatheken ist bei Dipteren weit verbreitet. Hier können prinzipiell zwei Erklärungen vorgeschlagen werden. Eine starke Lichtabsorption im sichtbaren und ultravioletten Bereich könnte die gespeicherten Spermatozoen vor mutagener Strahlung schützen. Dieser Schutz ist jedoch bereits durch die sklerotisierte Körperwand gewährleistet. Wahrscheinlicher ist, daß die Sklerotisierung zur Versteifung der Spermathekenkapseln dient. Einen Schutz vor mechanischer Verletzung benötigen die im Körperinneren gelegenen Spermatheken nicht, auch setzen keine Muskeln daran an. Die Versteifung der Kapselwand könnte jedoch der Fixierung des Spermathekenvolumens dienen, so daß Druckschwankungen innerhalb der Spermatheken einen Flüssigkeitstransport durch die Spermathekengänge bewirken. Diese Möglichkeit ist bei Überlegungen zur Funktionsweise der Spermatheken zu berücksichtigen.

Die Cuticula wird von einem flachen, unauffälligen Epithel gebildet. Unter dieses Epithel eingesenkt liegen große Kanaldrüsenzellen, von denen je eine mit einem Spermathekendorn assoziiert ist. Sie besitzen einen sehr großen Kern mit grobscholligem Chromatin und deutlichem Nucleolus. Ihr Cytoplasma ist reich an rauhem endoplasmatischem Retikulum und an freien Ribosomen, und erscheint dadurch besonders dicht. Jede Drüsenzelle umschließt mit einem apikalen Mikrovillisaum ein extrazelluläres Reservoir, in dem ein Drüsenendapparat liegt (Abb.19—21). Der Drüsenendapparat
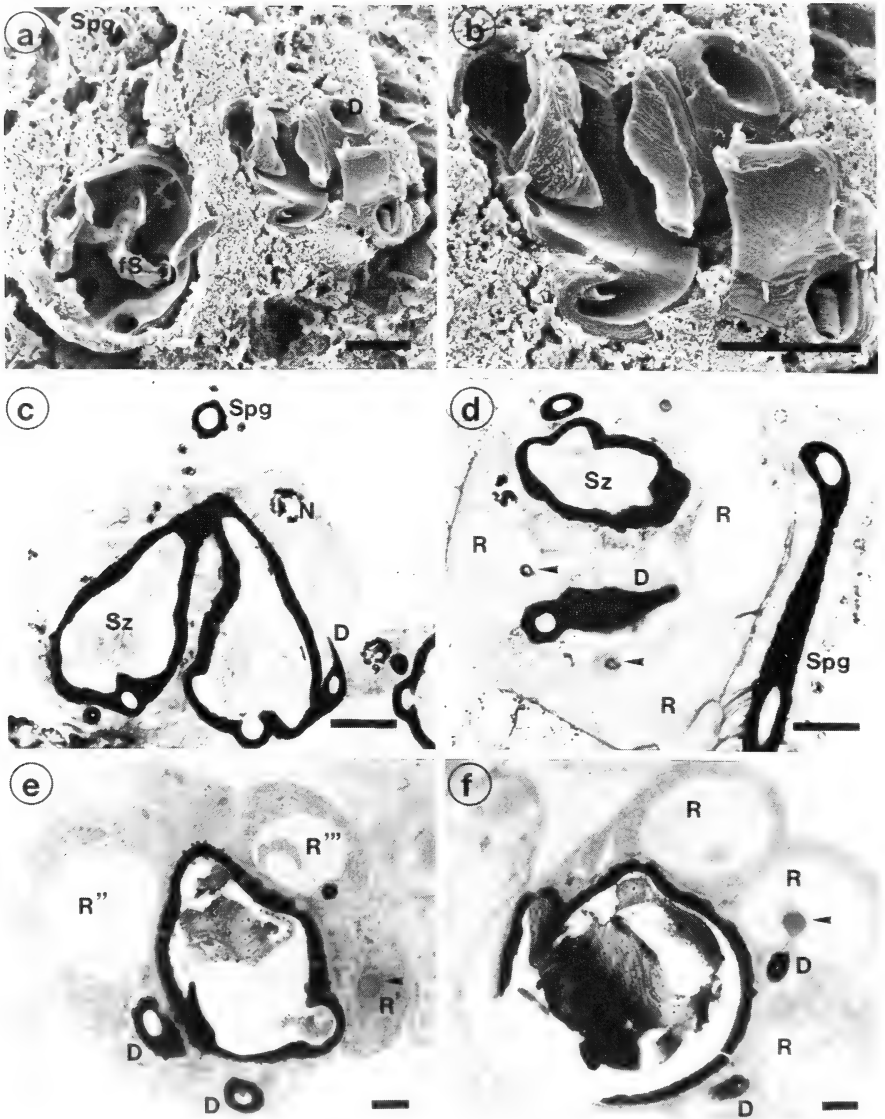
Abb.19: Spermatheken von *C. whitei*. (a) Blick auf zwei aufgebrochene Spermatheken, REM; (b) stärkere Vergrößerung von (a) zeigt den geschichteten Aufbau der Cuticula; (c—f) Semidünnschnitte, Richardson.

D: Dornenförmiger Fortsatz der Spermathek, fS: filamentöse Substanz, N: Nucleus, R, R'-R''': Drüsenreservoirs mit verschiedenem Inhalt, Spg: Spermathekengang, Sz: Spermatozoen, Pfeile: Drüsenendapparate, Balkenlänge jeweils 20 μm.
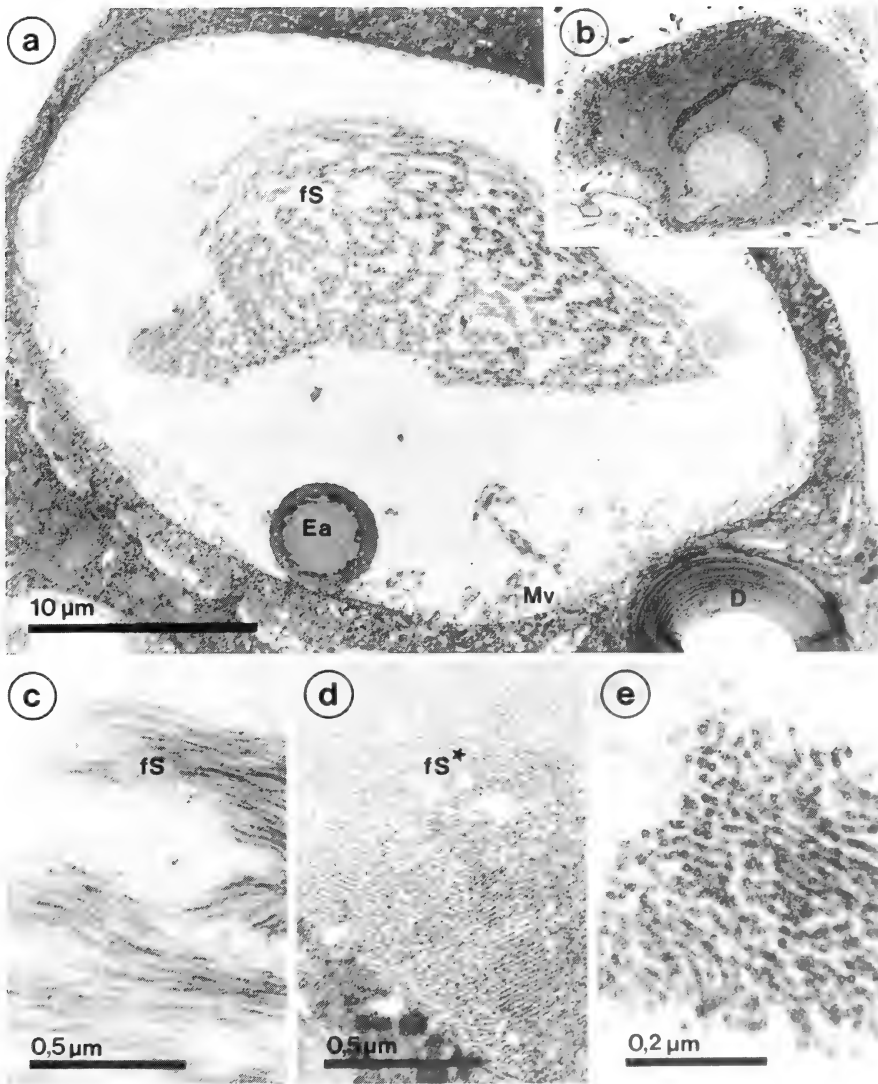
Abb.20: Drüsenreservoirs an den Spermatheken von *C. whitei*, TEM. (a) großes Drüsenreservoir (R'''); (b) kleines Drüsenreservoir (R', gleiches Objekt wie in Abb.21a) in gleicher Vergrößerung wie (a); (c) Ausschnittsvergrößerung der filamentösen Substanz aus (a); (d) Ausschnittsvergrößerung der pseudokristallin angeordneten Substanz in (b); (e) eine noch stärkere Vergrößerung des Inhalts eines großen Reservoirs zeigt die tubuläre Ultrastruktur der filamentösen Substanz.

D: dornenförmiger Fortsatz der Spermathek, Ea: Drüsenendapparat, fS: filamentöse Substanz, fS*: filamentöse Substanz in pseudokristalliner Anordnung, Mv: Mikrovillisaum.
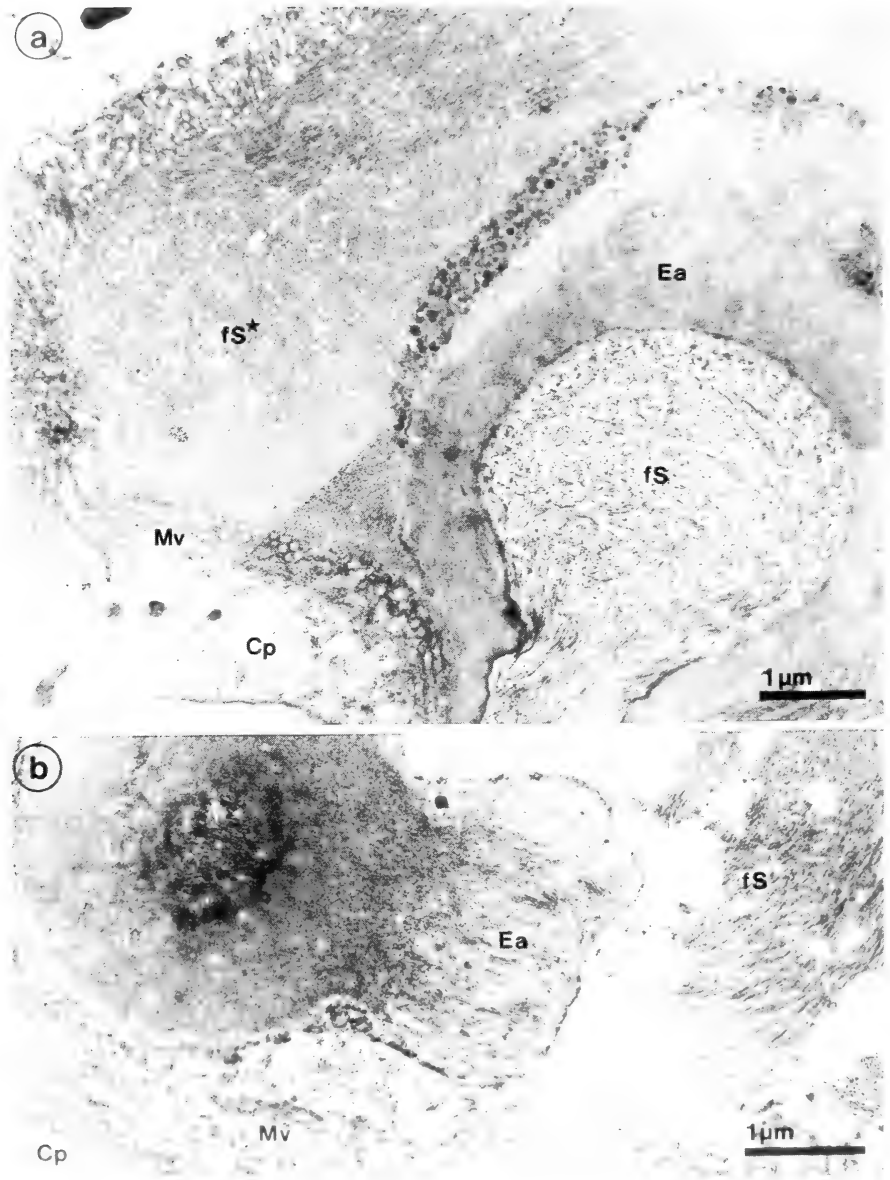
Abb.21: Drüsenendapparate an den Spermatheken von *C. whitei*, TEM. (a) Endapparat in einem kleinen Drüsenreservoir mit pseudokristallinem Inhalt (gleiches Objekt wie in Abb.20b); (b) Endapparat in einem großen Drüsenreservoir.

Cp: Cytoplasma, Ea: Drüsenendapparat, fS: filamentöse Substanz, fS*; filamentöse Substanz in pseudo-kristalliner Anordnung, Mv: Mikrovillisaum.

besteht aus einem runden Cuticulabläschen (Durchmesser 0,4—0,5 µm), das auf einer Seite von einer filzartigen Struktur bedeckt ist, während die andere Seite über einen feinen Cuticulagang mit dem Spermathekenlumen in Verbindung steht. Umfang und Inhalt der Drüsenreservoirs können sehr unterschiedlich sein. Lichtmikroskopisch erscheint der Inhalt basophil, homogen oder schollig, oder aber optisch leer. Im TEM enthalten alle Reservoirs röhrenförmige Filamente von ca. 10 nm Durchmesser, die in unterschiedlichem Maße aggregiert sind (Abb.20, 21). In kleinen Reservoirs (R', ca. 8 µm Durchmesser) liegen die Filamente so dicht gepackt, daß eine fast kristalline Struktur (fS*) entsteht. In großen Reservoirs hingegen, die im Nativpräparat die Spermathek an Durchmesser übertreffen können (über 50 µm Durchmesser), sind die Filamente gleichmäßig in einer Flüssigkeit verteilt (R'') oder zu Schollen zusammengelagert (R'''). Kleine und große Reservoirs können gleichzeitig nebeneinander an einer Spermathek vorkommen (Abb.19e). Filamentöse Strukturen, die denen in den Drüsenreservoirs gleichen, liegen auch innerhalb der Drüsenendapparate (Abb.21a).

Zum Hämolymphraum hin liegen die Drüsenzellen einer weniger als 0,05 µm dicken Basallamina auf, stellenweise sind sie von Fettgewebe umgeben. Im Bereich der Spermathekenkapseln ist keinerlei Muskulatur vorhanden. Auch eine Innervierung konnte im Bereich der Spermathekenkapseln nicht nachgewiesen werden.

Es liegen bereits von mehreren Dipterenarten vergleichbare elektronenmikroskopische Befunde der Drüsenzellen an den Spermatheken vor (*Aedes aegypti* (Clements & Potter 1967), *Drosophila melanogaster* (Filosi & Perotti 1975), *Glossina morsitans* (Kokwaro et al. 1981), *Dacus oleae* (Solinas & Nuzzaci 1984)). Es handelt sich dabei um Kanaldrüsenzellen (Noirot & Quennedey 1974 („class 3 gland cells"), Weidner 1982, Davey 1985)). Unterschiede fallen besonders hinsichtlich des Inhalts und Umfanges der Reservoirs („secretory cavity") auf. Bei *Aedes*, *Drosophila*, *Dacus* und *Glossina* reicht der dicht gepackte Mikrovillisaum der Drüsenzellen bis an das Filzwerk („feltwork") heran, welches das erweiterte Endstück des cuticulären Ausführganges umgibt. Bei *C. whitei* hingegen liegt zwischen dem Mikrovillisaum und dem, das Cuticulabläschen abschließenden Filzwerk eine große Menge der filamentösen Substanz (Durchmesser der tubulären Filamente ca. 10 nm), entweder in einem größeren Flüssigkeitsvolumen verteilt, oder in dichter, fast kristalliner Anordnung. Die Verbindung zwischen der filamentösen Substanz im Reservoir, dem Filzwerk des Endapparates und dem filamentösen Inhalt der Ausführkanäle und der Spermatheken (s. u.) ist noch zu klären. Weidner (1982) erwähnt röhrenförmige Fibrillen von 10—20 nm Durchmesser als Wandbestandteil des von der Drüsenzelle gebildeten Endapparates. Bei *Aedes* enthalten die Ausführkanäle zuweilen ein geordnetes, kristallin erscheinendes Material, welches aus dem Filzwerk hervorzugehen scheint (Clements & Potter 1967). Bei *Drosophila* hingegen ist das Sekret in den Drüsenreservoirs und den Spermatheken in parallelen Laminae von ca. 8 nm Durchmesser organisiert (Filosi & Perotti 1975).

Große Mengen an rauhem endoplasmatischen Retikulum deuten darauf hin, daß das Sekret der Drüsenzellen Eiweißkomponenten enthält (Pal & Ghosh 1982). Auch im Drüsensekret der Spermatheken von *Glossina morsitans* wurden, neben Mucopolysacchariden, Proteine nachgewiesen (Kokwaro et al. 1981). Zur Funktion des Sekrets gibt es verschiedene Annahmen: Es könnte Spermatozoen anlocken, ernähren, ruhigstellen, aktivieren oder zur Besamung der Eier aus den Spermatheken hinausschwemmen (Brüel 1897, Davey 1965, Lensky & Schindler 1967, Parker 1970, Tobe & Langley 1978, Weidner 1982). Möglicherweise ist das Sekret der Spermatheken auch zur Lebenderhaltung der Spermien im ventralen Receptaculum notwendig, wie es bei *Drosophila*

melanogaster nachgewiesen wurde (Anderson 1945). Filosi & Perotti (1975) halten bei *Drosophila melanogaster* eine zyklische Aktivität der Drüsenzellen für möglich. Dadurch ließe sich erklären, daß bei *C. whitei* Reservoirs so unterschiedlichen Ausmaßes und Inhalts nebeneinander vorliegen.

Inhalt der Spermatheken

Die Spermatheken unbegatteter Weibchen enthalten eine basophile, filamentöse Substanz, die dem Inhalt des ventralen Receptaculum gleicht. Bei begatteten Weibchen enthalten alle drei Spermatheken Spermatozoen, die meist parallel zueinander in Knäueln oder Wirbeln liegen (Abb.19c,d). In Zupfpräparaten in Insektenringer oder Wasser sind die Spermatzoen sofort beweglich (s. „Spermatozoen").

In den Spermatheken von *C. whitei* können die Spermatozoen mindestens 7 Wochen lang befruchtungsfähig bleiben (eigene Untersuchungen). Bei *Glossina morsitans* ist eine Speicherung über 200 Tage (Saunders & Dodd 1972), bei der Honigbiene sogar über mehrere Jahre (Lensky & Schindler 1967) möglich.

Die Befunde aus den Nativpräparaten von *C. whitei*-Spermatheken scheinen zunächst gegen eine Inaktivierung der Spermatozoen während der Speicherzeit zu sprechen. Doch kann eine Wiederherstellung der Beweglichkeit in kürzester Zeit durch den mit der Präparation verbundenen Milieuwechsel nicht ausgeschlossen werden. Laut Lensky & Schindler (1967) liegen die Spermatozoen in der Spermathek der Honigbiene in bewegungslosen Bündeln vor und werden erst durch das Sekret der Spermathekaldrüsen aktiviert, wobei es sich schlichtweg um eine Folge der Verdünnung handeln soll. Ein vergleichbarer Effekt wäre auch in den Nativpräparaten von *C. whitei* denkbar.

Spermathekengänge

Die Ausführgänge der Spermatheken sind ca. 350 μm lang, ihr Lumen hat einen Durchmesser von 5,3—6,7 μm. Im distalen Drittel ist die Cuticula bei einer Höhe von ca. 1,7 μm stark sklerotisiert und schwarz wie die der Spermatheken selbst (Abb.18, 22a). Sie liegt einem kubischen Epithel auf, das basal nur durch eine ca. 0,05 μm dicke Basalmembran vom Hämolymphraum abgegrenzt ist. Die apikale Cytoplasmamembran bildet durch zahlreiche Einfaltungen auffällige Membranstapel. Die quer zur Richtung des Ganges parallel angeordneten Membranen verlaufen senkrecht von der Zelloberfläche ins Cytoplasma hinein (Abb.22b—d). Sie sind an der cytoplasmatischen Seite dicht mit elektronendichten Partikeln von ca. 9 nm Durchmesser besetzt (Abb.22c). Zwischen den Membranstapeln liegen zahlreiche Mitochondrien.

In zwei Arbeiten von Kokwaro et al. (1981, 1988) über *Glossina morsitans* findet man ähnliche Stapel aus asymmetrischen Membranen abgebildet. Sie befinden sich zum einen in Epithelzellen, die zwischen den Kanaldrüsenzellen des Spermathekenepithels liegen, zum anderen in dem Epithel, welches den Ductus ejaculatorius der Männchen umgibt. Auch hier sind die aus apikalen Membraneinfaltungen hervorgegangenen Membranstapel von zahlreichen Mitochondrien gesäumt.

Laut Davey (1985) lassen mit Mitochondrien assoziierte, apikale Cytoplasmamembraneinfaltungen, wie sie im Spermathekenepithel verschiedener Insekten zu finden sind, auf eine hohe Ionentransportaktivität schließen. Bei partikelbesetzten Membranstapeln aus apikalen Cytoplasma-

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Abb.22: Spermathekengänge von *C. whitei*. (a) Semidünnschnitt, Richardson, distaler Abschnitt des Spermathekenganges links, proximaler Abschnitt rechts; (b) Ultradünnschnitt aus dem distalen Bereich, TEM; (c—d) Ausschnittsvergrößerungen der aus apikalen Cytoplasmamembraneinfaltungen gebildeten Membranstapel in (b).
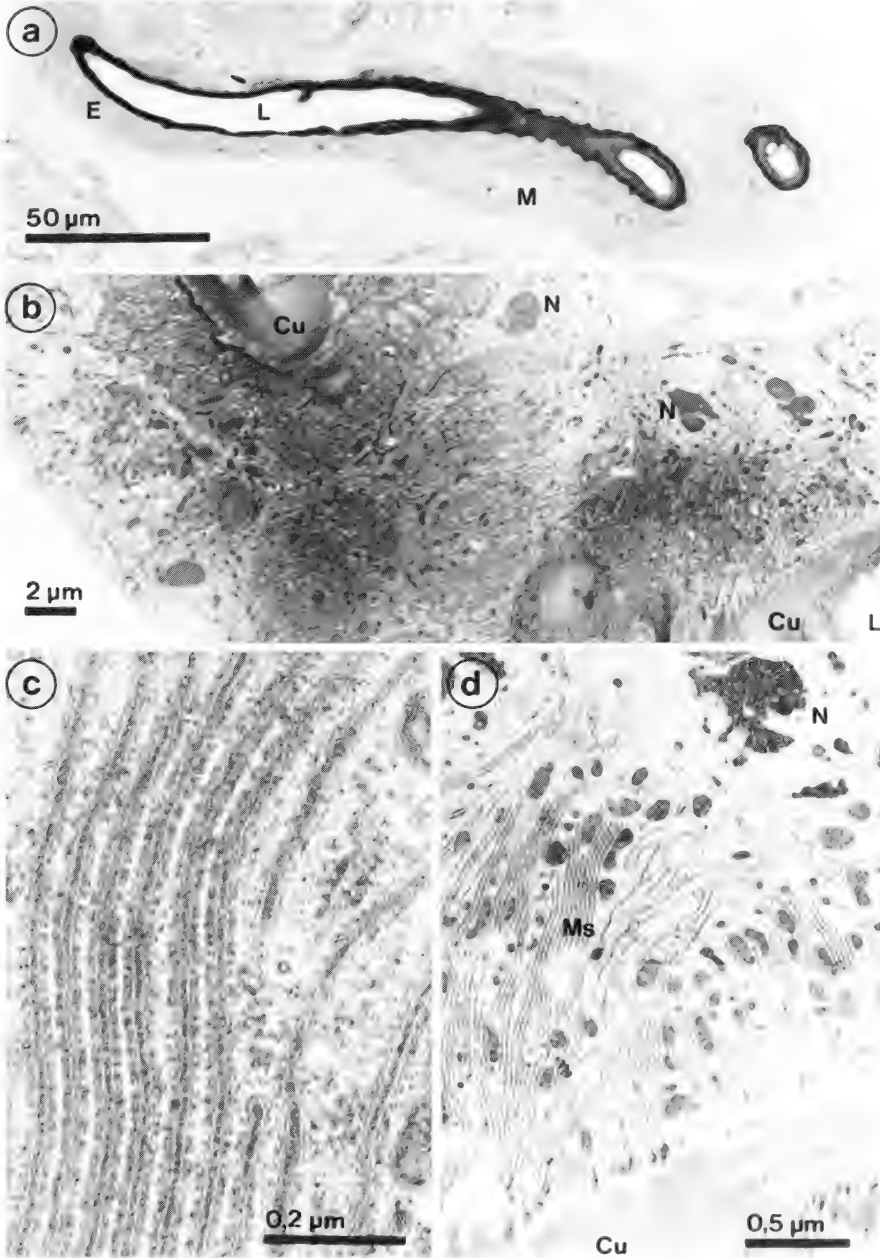
Cu: Cuticula, E: Epithel, L: Lumen des Spermathekenganges, M: Längsmuskulatur, Ms: Membran-
stapel, N: basal gelegene Nuclei des Epithels.

membraneinfaltungen im Mitteldarm von *Manduca sexta* und in den Hüllzellen von Insektensensillen konnte in den Partikeln eine Protonen-Kalium-Antiport-ATPase nachgewiesen werden (Klein & Zimmermann 1991). Wenn auch an den Membranstapeln der Spermathekengänge bei *C. whitei* ein Transport von Protonen und/oder Kaliumionen stattfände, so wäre an eine Regulation der Spermatozoenbeweglichkeit zu denken, welche bekanntlich stark von der Konzentration dieser Ionen abhängt (Baccetti & Afzelius 1976). Eine weitere Untersuchung der Funktion dieser Epithelzellen könnte möglicherweise wesentlich zur Klärung der Transportmechanismen im Bereich der Spermatheken beitragen.

Im restlichen, proximalen Teil der Spermathekengänge ist die Cuticula nicht sklerotisiert und ca. 2,5 μm dick. Die dem Epithel zugewandte Seite trägt unregelmäßige, quer verlaufende Rippen, während die apikale Oberfläche der Cuticula überall in den Spermathekengängen glatt ist. Das Epithel ist basal von einer dicht innervierten, einschichtigen Längsmuskulatur umgeben (Abb.9, 12A, 22a, 26e), Ringmuskulatur fehlt. Dementsprechend führen die Spermathekengänge im Nativpräparat nickende Bewegungen aus, während eine peristaltische Verengung der ohnehin dickwandigen Spermathekengänge nie beobachtet wurde.

Einige Autoren halten es für möglich, daß die Muskulatur der Spermathekengänge für einen aktiven Spermatozoentransport in die Spermatheken verantwortlich sei (Wigglesworth 1974, Jones & Fischman 1970, Solinas & Nuzzaci 1984). Die Spermathekengänge von *C. whitei* sind nicht zu peristaltischen Bewegungen fähig. Es ist schwer vorstellbar, daß die durch Längsmuskulatur hervorgerufenen, nickenden Bewegungen sich nennenswert auf das Lumen der dickwandigen Gänge auswirken und so beim Spermatransfer eine mehr als unterstützende Rolle spielen könnten. Es ist aber auch keine andere naheliegende Hypothese für die Funktion dieser relativ stark entwickelten Längsmuskelschicht bekannt.

Die Spermathekengänge vereinigen sich wenige μm vor ihrer Mündung am Grund der ca. 50 μm hohen Genitalpapille (Abb.12E—I). An der Vereinigungsstelle der Gänge ist die Cuticula besonders dicht und bildet zudem einen in das Ganglumen vorspringenden Wulst. Je nachdem, ob die Genitalpapille im Zuge von Verschiebungen des Vaginaepithels craniad oder caudad gerichtet ist, verschließt dieser Wulst die Mündung der Spermathekengänge vollständig (Abb.10b) oder nur teilweise (Abb.38b). Zudem ist an der cranialen Seite der Genitalpapille in der Nähe der Spermathekengangmündung eine verfestigte Cuticulaplatte ausgebildet (Abb.10b, d), die bei der Kontraktion seitlich ansetzender Muskelfasern (MGp) auf den Cuticulawulst drücken und so die Mündung verschließen kann.

Verschiebungen des Vaginaepithels, wie sie während der Kopulation und der Eiablage (s. dort) in beträchtlichem Maße stattfinden, können rein mechanisch die Öffnung der Spermathekengänge regulieren. Ein aktives Verschließen der Spermathekengänge ermöglicht darüberhinaus eine sofortige Unterbrechung der Spermaabgabe aus den Spermatheken und damit eine Minimierung von Spermaverlusten. Es könnte dem Weibchen aber auch ermöglichen, den Spermatransfer aus einer Spermatophore (s. dort) zu verhindern und so noch nach vollzogener Kopulation weibliche Zuchtwahl auszuüben („cryptic female choice" (Thornhill & Alcock 1983)).

Abb.23: Akzessorische Drüse von *C. whitei.* (a) Semidünnschnitt, Richardson; (b) TEM; Einsatz: Ausschnittsvergrößerung aus (b).

Cu: Cuticula, Ea: Drüsenendapparat, L: Drüsenlumen, mP: muskulöse Pumpe, N: Nucleus, Nv: Nerv, R: Drüsenreservoir, S: Sekret.

(a) Cu L S Nv mP 50 μm

(b) N R L Ea R Ea 10 μm

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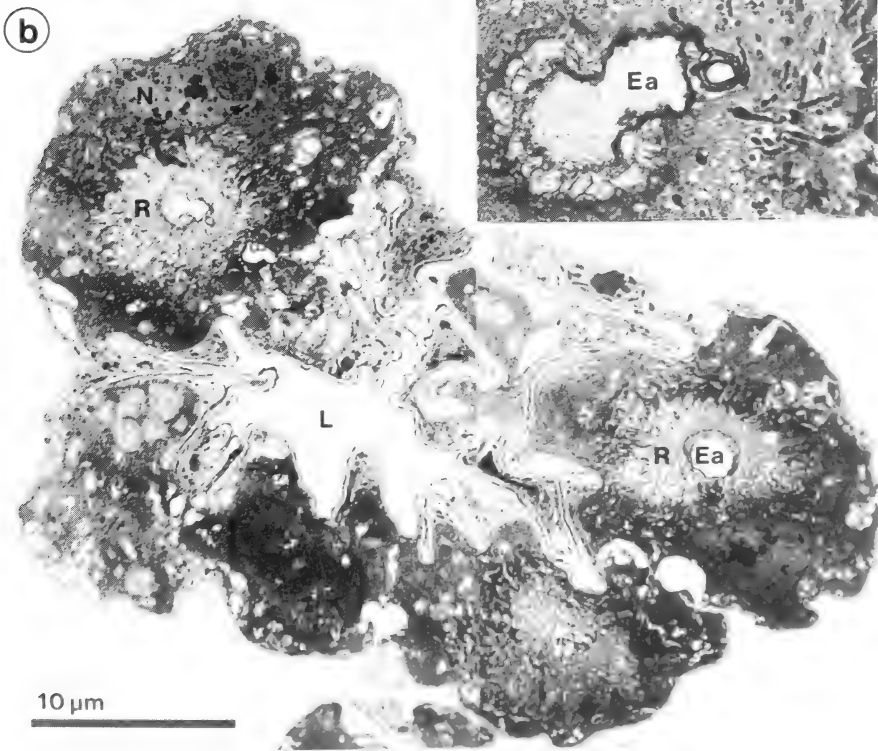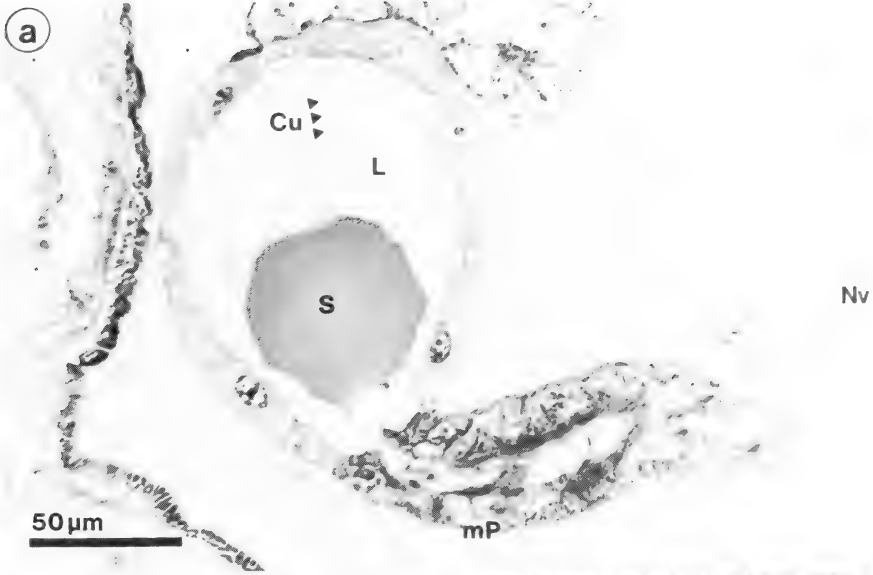
Akzessorische Drüsen

Die akzessorischen Drüsen von *C. whitei* sind im Nativpräparat als ein Paar farbloser, eiförmiger Bläschen zu erkennen. Ihre dünnwandigen Ausführgänge münden caudal von denen der Spermatheken in die Genitalpapille (Abb.8). Während die akzessorischen Drüsen selbst mit keinerlei Muskulatur und Innervierung versehen sind, ist im distalen Bereich ihrer Ausführgänge eine reichlich innervierte muskulöse Pumpe ausgebildet.

Das Drüsenlumen ist ca. 100x150 μm groß und von einer zarten, nur ca. 0,2 μm hohen Cuticula ausgekleidet (Abb.23), die einem flachen Epithel aufliegt. Unter das Epithel eingesenkt liegen pro Drüse etwa 15 Kanaldrüsenzellen, die sich durch große Kerne, zahlreiche Mitochondrien und elektronendichtes Cytoplasma auszeichnen. Jede Drüsenzelle umschließt mit einem apikalen Mikrovillisaum ein extrazelluläres Reservoir, in dem ein cuticulärer Drüsenendapparat von ca. 2—3 μm Durchmesser liegt. Das Drüsensekret ist lichtmikroskopisch homogen basophil und im TEM auch bei 20 000facher Vergrößerung amorph. Es erscheint in den Reservoirs wesentlich elektronendichter als in den Endapparaten und im Drüsenlumen. Spermatozoen wurden im Bereich der akzessorischen Drüsen nie gefunden.

Ein Vergleich der Kanaldrüsenzellen an Spermatheken und akzessorischen Drüsen (vergl. Abb.21 und 23 b) zeigt, daß die Drüsenendapparate an den akzessorischen Drüsen kleiner und wesentlich dünnwandiger sind, das sie bedeckende Filzwerk viel lockerer. Diese ultrastrukturellen Unterschiede hängen wahrscheinlich mit der unterschiedlichen Natur der Sekrete zusammen.

Die Ausführgänge der akzessorischen Drüsen sind ca. 350 μm lang. Ihr Lumen nimmt von proximal ca. 5 μm Durchmesser nach distal allmählich auf das doppelte zu und bildet dann im letzten Viertel eine Erweiterung von bis zu 20 μm Durchmesser, um schließlich über eine Engstelle mit dem terminalen Drüsenlumen in Verbindung zu stehen. Die quergefältelte Intima ist im proximalen Bereich ca. 0,5 μm dick und kann hier leicht sklerotisiert sein, im distalen Bereich der Gänge ist sie mit nur 0,2 μm Höhe so zart wie in den Drüsen selbst. Eine dünne Muskelschicht umgibt die Gänge auf ihrer gesamten Länge (Abb.12A) und befähigt sie im Nativpräparat zu schlängelnden Bewegungen. Um den distalen, erweiterten Bereich herum ist die Muskulatur besonders stark ausgebildet und innerviert (Abb.23a).

Die Ausführgänge der akzessorischen Drüsen münden getrennt, durch schmale Spalten in die caudale Wand der Genitalpapille (Abb.12I—K). Es ist keine Ventilstruktur ausgebildet.

Der erweiterte distale Bereich der Ausführgänge stellt mit seiner reich innervierten Ringmuskulatur offensichtlich eine Pumpe dar, wie sie auch bei Tephritiden beschrieben ist (Solinas & Nuzzaci 1984).

Da die Ausführgänge der akzessorischen Drüsen direkt gegenüber vom Eingang des ventralen Receptaculum münden, könnte ihr Sekret beim Befruchtungsvorgang eine Rolle spielen (s. „ventrales Receptaculum" und „Eiablage"), wie es für *Musca domestica* nachgewiesen wurde (Leopold & Degrugillier 1973, Leopold 1980). Es ist hingegen unwahrscheinlich, daß das Sekret der akzessorischen Drüsen zum Festkleben der Eier bei der Eiablage dient, wie es von verschiedenen Autoren für andere Dipteren vorgeschlagen wurde (Brüel 1897, Wesché 1906, Mote 1929, Jahn 1930, Gra-

ham-Smith 1938, Pandey & Agrawal 1962, Fowler 1973, McAlpine 1981). Die tatsächlich am Substrat festgeklebte Unterseite des Eies kommt während der Eiablage in der Vagina ventral, also von der Mündung der akzessorischen Drüsen abgewandt, zu liegen. Ebenfalls unwahrscheinlich ist, daß das Sekret zur Ernährung der Spermien (Gilbert 1986) oder als Medium für den Spermatozoentransport in den Spermathekengängen (Solinas & Nuzzaci 1984) dient. Es ist kein Mechanismus bekannt, durch den das Sekret der akzessorischen Drüsen gezielt in die Spermathekengänge befördert werden könnte.

Innervierung

Das hinterste Ganglion von *C. whitei*, das Abdominalganglion, liegt in dem sehr schlanken cranialen Abschnitt des Abdomen. Von dort führt ein unpaarer ventraler Abdominalnerv median caudad (Abb.3b). Er gibt in seinem Verlauf mehrere Seitennerven ab und tritt schließlich zwischen den beiden lateralen Ovidukten hindurch auf die Dorsalseite des Oviductus communis. Dort spaltet sich der Abdominalnerv in zwei Nervenstämme, die beiderseits dorsolateral an der Vagina entlang bis in die Cerci hinein ziehen. Die Ovarien und Ovidukte sind vom unpaaren Teil des Abdominalnervs her innerviert, der restliche Teil der inneren weiblichen Geschlechtsorgane und der Endabschnitt des Darmes von den beiden dorsolateralen Nervenstämmen. Die genaue Topographie
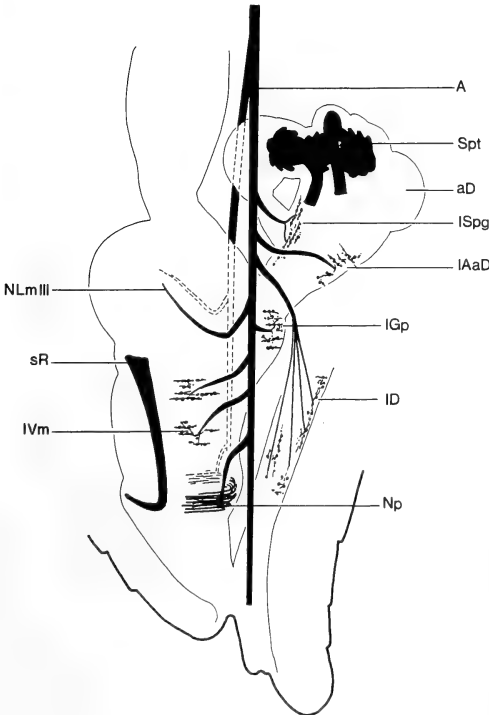
Abb.24: Innervierung der inneren weiblichen Geschlechtsorgane von *C. whitei*, Lateralansicht von links, stark vereinfacht. Der Übersichtlichkeit wegen ist nur der linke Nervenstamm mit seinen wichtigsten Abzweigungen durchgehend abgebildet.

A: Aufzweigung des Abdominalnerven in zwei dorsolaterale Stämme, aD: Akzessorische Drüse, IAaD: Innervierung der Ausführgänge der akzessorischen Drüsen, ID: Innervierung des Darmes, IGp: Innervierung der Genitalpapille, ISpg: Innervierung der Spermathekengänge, IVm: Innervierung der Vaginamuskulatur, NLmIII: Nervenast entlang des Muskels Lm III, Np: Nervenplexus, Spt: Spermathek, sR: sklerotisierter Ring.

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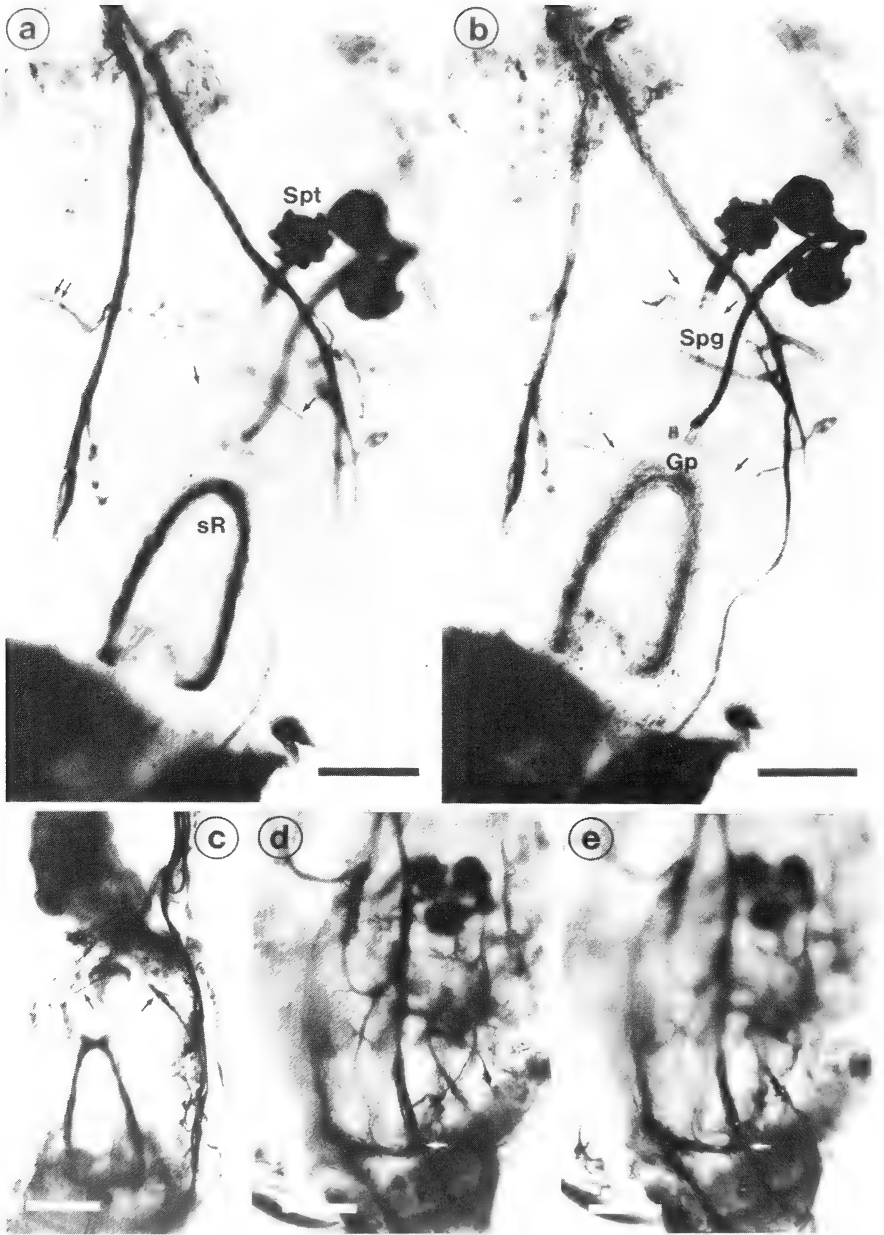
Abb.25: Innervierung der inneren weiblichen Geschlechtsorgane von *C. whitei*. (a) Dorsalansicht eines Totalpräparats mit CoCl$_2$-Füllung, auf ventrale Seite der Vagina fokussiert, Pfeile: Nervenäste entlang der Muskeln Lm III und Innervierung des Darmes; (b) dasselbe Präparat, auf dorsale Seite der Vagina

der Nervenverzweigungen im Bereich der inneren weiblichen Geschlechtsorgane von *C. whitei* ist individuell unterschiedlich, das hier beschriebene Grundschema der Innervierung (Abb.24) bleibt jedoch erhalten.

Zahlreiche Nervenendknöpfchen („boutons") an den Muskelfasern der Ovidukte und der Vagina, besonders aber im Bereich der Genitalpapille und der Ausführgänge von Spermatheken und akzessorischen Drüsen, weisen auf eine reichliche motorische Innervierung hin (Abb.26). Hingegen konnte im Bereich der Spermathekenkapseln, der akzessorischen Drüsen selbst und des vom sklerotisierten Ring eingefaßten Epithelpolsters keine Innervierung nachgewiesen werden.

Zwei Nervenäste treten dorsolateral in die Vagina ein und begleiten die Muskeln Lm III auf ihrem Weg bis in die Nähe des ventralen Receptaculum (Abb.25a,c), erreichen jedoch nicht dessen Cuticulakammern oder -borsten. Desweiteren umspannt den dorsalen Teil der Vagina auf Höhe des caudalen Endes des sklerotisierten Ringes ein in die Ringmuskulatur eingebetteter Nervenplexus, der auf beiden Seiten mit den dorsolateralen Nervenstämmen in Verbindung steht und mit einigen Perikaryen assoziiert ist (Abb.25d,e, 26a,c,d). Endknöpfchen werden von diesen Nerven nicht ausgebildet.

Die Innervierung der inneren weiblichen Geschlechtsorgane von Dipteren ist bisher nur oberflächlich untersucht worden (Polovodova 1953, Degrugillier & Leopold 1972, Bennettová & Mazzini 1989). So fand ein Nervenplexus im caudalen Bereich der Vagina, wie er bei *C. whitei* durch die Füllung mit CoCl$_2$ dargestellt werden konnte, anscheinend bisher keine Erwähnung. Wahrscheinlich handelt es sich um einen von multiterminalen sensorischen Neuronen gebildeten Dehnungsrezeptor (Finlayson 1968), der den Dehnungsgrad der Vaginamuskulatur bei der Kopulation bzw. Eiablage registriert. Eine ähnliche Deutung könnte auch für die Nervenäste entlang der Muskeln Lm III zutreffen.

Eine fehlende Innervierung der Spermathekendrüsen steht in Einklang mit Befunden anderer Autoren (Degrugillier & Leopold 1972, Jones & Fischman 1970, Noirot & Quennedy 1974). Ein fehlender Nachweis einer Innervierung, beispielsweise im Bereich des ventralen Receptaculum, kann jedoch noch nicht als Beweis für das Fehlen jeglicher Innervierung ausreichen. Man kann nicht mit Sicherheit davon ausgehen, daß mit der angewandten Methode auch in der Tiefe des Gewebes alle Nervenendigungen dargestellt wurden.

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fokussiert, Pfeile: Innervierung der Spermathekengänge und der Genitalpapille; (c) Ventralansicht eines Totalpräparats mit silberverstärkter CoCl$_2$-Füllung, Pfeile: Nervenäste entlang der Muskeln Lm III; (d—e) Dorsalansicht eines Totalpräparats mit silberverstärkter CoCl$_2$-Füllung, unterschiedlich fokussiert, Pfeile: Nervenplexus in der dorsalen Wand der Vagina.

Gp: Genitalpapille, Spg: Spermathekengänge, Spt: Spermatheken, sR: sklerotisierter Ring, Balkenlänge jeweils 100 μm.
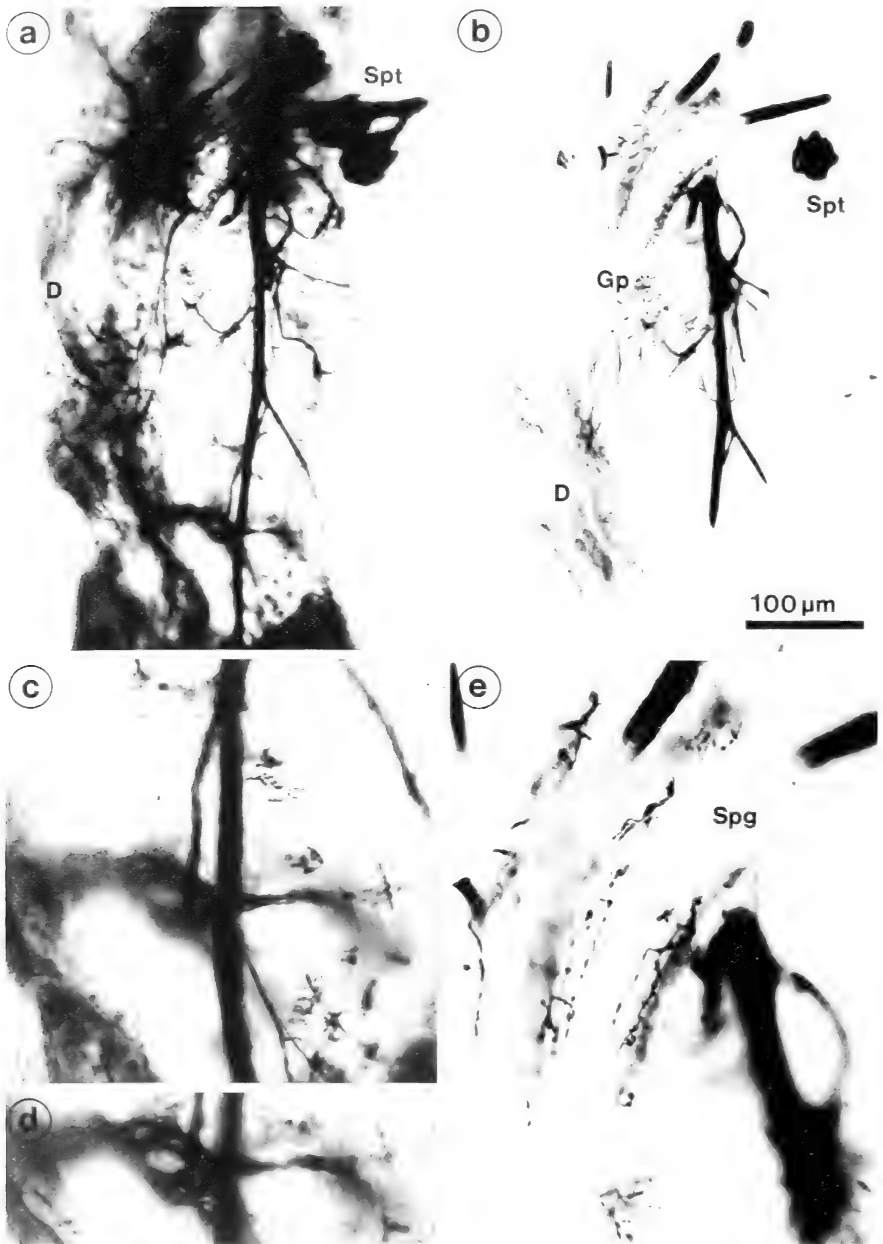
Abb.26: Innervierung der inneren weiblichen Geschlechtsorgane von *C. whitei*. (a) Lateralansicht eines Totalpräparats mit silberverstärkter CoCl₂-Füllung von rechts; (b) dasselbe Präparat im Dickschnitt (5

MÄNNLICHES REPRODUKTIONSSYSTEM

Äußere männliche Geschlechtsorgane

Abb.2b,d zeigt das Abdomen eines *C. whitei*-Männchens von ventral in der Ruhelage. Am Ende des Abdomen sind die Cerci erkennbar, cranial davon das Periandrium, an dem ventrolateral die Gonostyli artikuliert sind. Der „innere Kopulationsapparat", der bei der Kopulation in die Vagina des Weibchens eingeführt wird, liegt in der Ruhelage in einer Tasche des Hypandrium an der Abdomenunterseite verborgen und wird zur Kopulation herausgeklappt (Abb.28d). Er besteht aus Aedeagus, Epiphallus und Phallophor (Abb.27). Über die Basis des Phallophor ist der innere Kopulationsapparat am caudalen Ende des Phallapodem artikuliert, welches von der Körperoberfläche in das männliche Abdomen hineinragt und so eine Verankerung bildet. Zwischen der Basis des Phallophor und dem Hypandrium bildet die Körperwand seitlich ein Paar membranöse Anhänge, die Postgonite.

In der Benennung der verschiedenen Teile der männlichen Geschlechtsorgane stimmen die bisherigen Bearbeiter nicht überein. Die hier gewählte Benennung folgt Feijen (1989), der in seiner Monographie über die Diopsidae deren äußere männliche Geschlechtsorgane beschrieben und dabei die gesamte bisherige Diopsidenliteratur berücksichtigt hat (Abb.27a bietet eine vergleichbare Ansicht für *C. whitei* wie Abb.66 aus Feijen (1989) für *Sphyracephala subbifasciata*). Überdies steht diese Benennung mit Griffiths' Werk über die Cyclorrhapha (1972) im Einklang. Der Begriff „Phallapodem" ist etwas irreführend, da nur der craniale Teil dieser Struktur als Apodem im engeren Sinne bezeichnet werden kann. Der caudale und der ventrale Arm liegen in der Körperoberfläche zwischen Hypandrium und Phallophor und sind somit als Sklerite zu verstehen, von denen aus sich das Apodem eingefaltet hat (Hennig 1958). Der Begriff „innerer Kopulationsapparat" folgt Hennig (1958).

Die Silhouette des Phallapodem erinnert von lateral gesehen an ein Gewehr, dessen kurzer Lauf nach caudal weist (Abb.27). Der craniale Teil bildet eine große Muskelansatzfläche, während der ventrale Fortsatz eine Verbindung zum Hypandrium herstellt. Der caudale Teil ist gegabelt und endet in zwei Gelenkhöckern, an denen der Phallophor artikuliert ist. Der Phallophor hat in etwa die Form eines offenen Ringes aus zwei Skleriten, zwischen denen hindurch der Ductus ejaculatorius verläuft. Der Aedeagus ist an seiner Basis relativ schlank, weiter außen trägt er eine bizarr geformte, membranöse Erweiterung (Abb.27, 28a,e, 29b,c,d). Er wird der Länge nach von einem Paar asymmetrischer Sklerite gestützt (Abb.29a), die am caudalen Teil des Phallophor inserieren. Terminal trägt der Aedeagus in Verlängerung des rechten Sklerits einen langen, gekrümmten Fortsatz mit einer hakenförmigen Spitze (Abb.27, 28e,f, 29a). Die Lage des Phallotrema, dorsal an der Basis des stabförmigen Fortsatzes, ließ sich sowohl im REM als auch anhand von Schnittserien nachweisen (Abb.28e, 29d). Ein Totalpräparat der männlichen Geschlechtsorgane nach einer unterbrochenen Kopulation weist eine an der

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µm); (c—d) Nervenplexus in der dorsalen Wand der Vagina, stärkere Vergrößerung von (a); (e) Innervierung der Spermathekengänge, stärkere Vergrößerung von (b).

D: Darm, Gp: Genitalpapille, Spg: Spermathekengänge, Spt: Spermatheken.
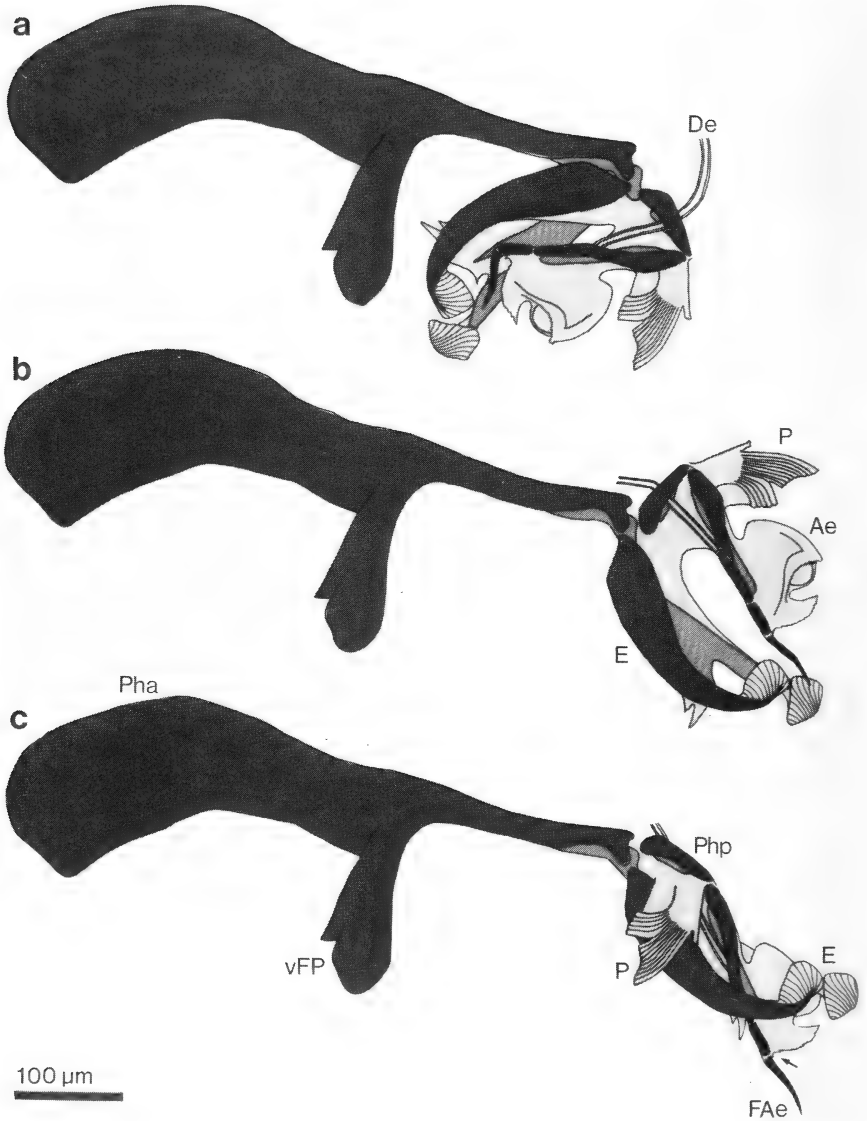
Abb.27: Phallapodem und innerer Kopulationsapparat von *C. whitei*-Männchen, Lateralansicht von links. Dunkle und bei paarigen Strukturen halbdunkle Schattierung kennzeichnet stark sklerotisierte Bereiche, helle Schattierung membranöse Bereiche. (a) eingeklappter Ruhezustand; (b) präparativ ausgeklappt; (c) maximal eregierter Zustand während der Kopulation.

Ae: Aedeagus, De: Ductus ejaculatorius, E: Epiphallus, FAe: Fortsatz des Aedeagus, P: Postgonit, Pha: Phallapodem, Php: Phallophor, vFP: ventraler Fortsatz des Phallapodem, Pfeil: Phallotrema.
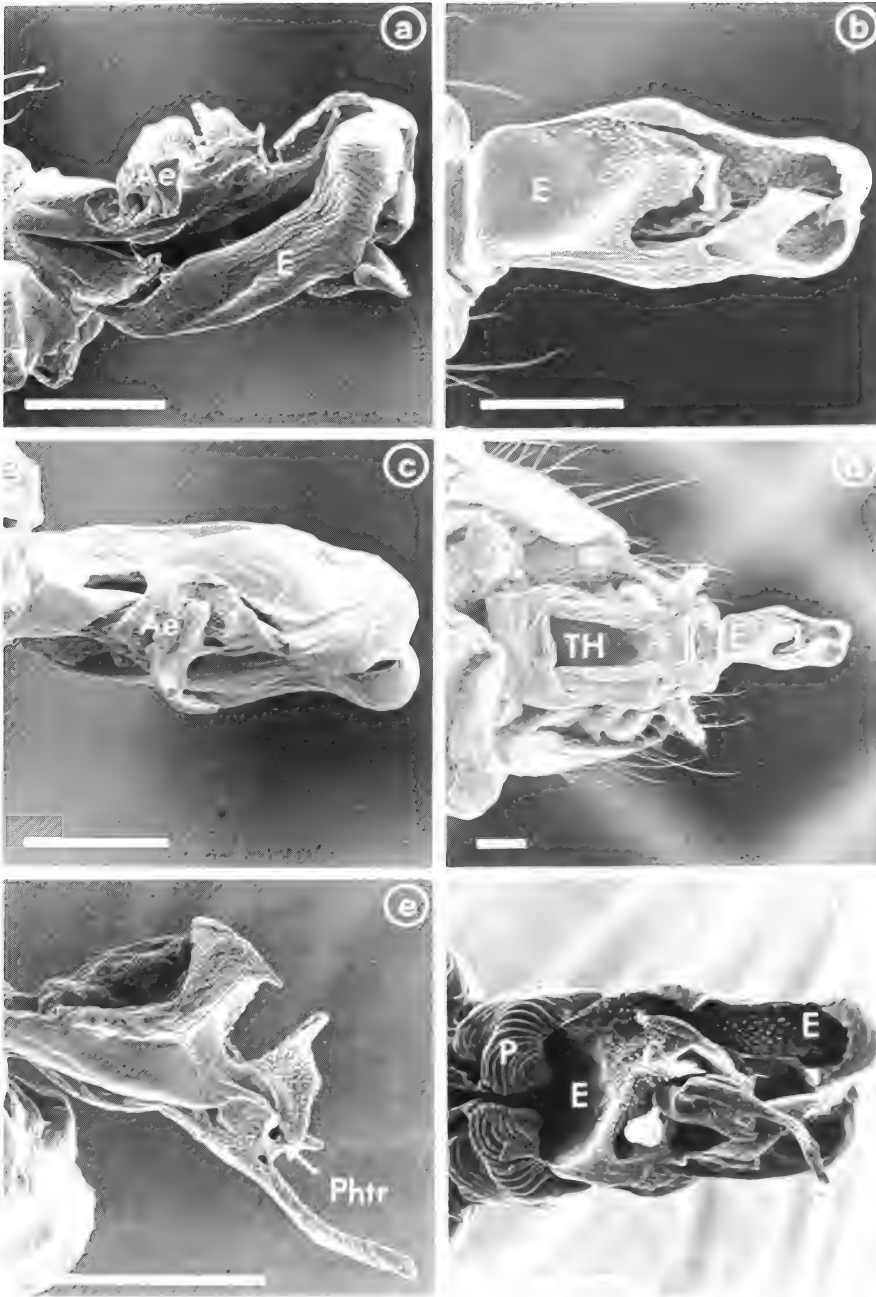
Abb.28: Innerer Kopulationsapparat von *C. whitei*, REM. (a) Präparativ ausgeklappt, Stellung wie in Abb.27b, Lateralansicht von links; (b) Ventralansicht desselben Präparats; (c) Dorsalansicht desselben Präparats; (d) Ventralansicht desselben Präparats; (e) freipräparierter Aedeagus, Lateralansicht von links; (f) maximal eregierter Kopulationsapparat, Stellung wie in Abb.27c, Ventralansicht.

Ae: Aedeagus, E: Epiphallus, FAe: stabförmiger Fortsatz des Aedeagus, P: Postgonit, Phtr: Phallotrema, TH: Tasche im Hypandrium, Balkenlänge jeweils 100 μm.

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Basis des Aedeagusfortsatzes tropfenförmig hervorquellende Masse auf (Abb.29b), deren Austrittsstelle die Lage des Phallotrema kennzeichnet.

Der Epiphallus bildet ein Paar zweilappiger Schaufeln (Abb.27, 28, 29a), deren membranöse Enden nach median eingekrümmt sind. Er wird der Länge nach von einem Paar Sklerite versteift, die am cranialen Teil des Phallophor inserieren. Die Cuticula von Aedeagus und Epiphallus bildet zahlreiche Wärzchen, röhrenförmige Vorsprünge und Riefen (Abb.28).

Die Postgonite enthalten keinerlei Sklerotisierungen, ihre membranöse Oberfläche ist durch parallele Rillen strukturiert.

Die äußeren Geschlechtsorgane erscheinen auf den ersten Blick nahezu symmetrisch. Bei genauer Betrachtung entdeckt man jedoch in allen Teilen geringe Asymmetrien. Besonders leicht zu erkennen ist die Asymmetrie der Sklerite im Aedeagus (Abb.29a). Bei 35 daraufhin untersuchten Männchen wurde immer eine gleichsinnige Asymmetrie festgestellt.

Die Asymmetrie der äußeren männlichen Geschlechtsorgane von *C. whitei* ist eine Folge der allen Cyclorrhaphen gemeinsamen Circumversion (Hennig 1973, McAlpine 1981, Bickel 1990): Das männliche Abdomenende wird noch innerhalb des Puparium irreversibel 360 ° im Uhrzeigersinn um die Körperlängsachse gedreht. Im Körperinneren ist diese Rotation durch die Windung des Ductus ejaculatorius um den Hinterdarm belegt.

Zur Kopulation wird der innere Kopulationsapparat um ca. 160 ° caudad ausgeklappt (vgl. Abb.2b,d, 28d), so daß Phallophor und Aedeagus fast in einer Linie mit dem Phallapodem zu liegen kommen. Die Postgonite umfassen die Basis des Aedeagus und bilden so eine kragenartige Struktur (Abb.27c, 28f). Der stabförmige Fortsatz des Aedeagus ragt zwischen den Schaufeln des Epiphallus hindurch nach ventral. Da das Postabdomen des Männchens bei der Kopulation ventrad eingekrümmt wird, kommt der Fortsatz in der Vagina des Weibchens schließlich dorsal zu liegen, die Schaufeln des Epiphallus ventral (Abb.36).

Das Einklappen des inneren Kopulationsapparates im Ruhezustand wurde von Griffiths (1972) für die Diopsiden beschrieben („Aedeagus ... able to be swung through wide arc against aedeagal apodeme to anteriorly directed rest position"). Dies konnte für *C. whitei* bestätigt werden, obwohl Feijen (1989) den „weiten Bogen" bei den Diopsidae s.str. für unzutreffend hält.

Innere männliche Geschlechtsorgane

Von den paarigen Hoden kommend, münden die Vasa deferentia gemeinsam mit einem Paar akzessorischer Drüsen in das distale Ende des Ductus ejaculatorius I, welches von einem Drüsenpolster umgeben ist (Abb.30). Der Ductus ejaculatorius I führt zur Spermapumpe, und diese mündet in den Ductus ejaculatorius II, der zum Phallotrema führt.

Abb.29: Innerer Kopulationsapparat von *C. whitei*. (a—b) Dorsalansicht eines nach unterbrochener Kopulation fixierten Totalpräparates, unterschiedlich fokussiert; (c—d) Aedeagus, mediane Semidünnschnitte, Richardson.
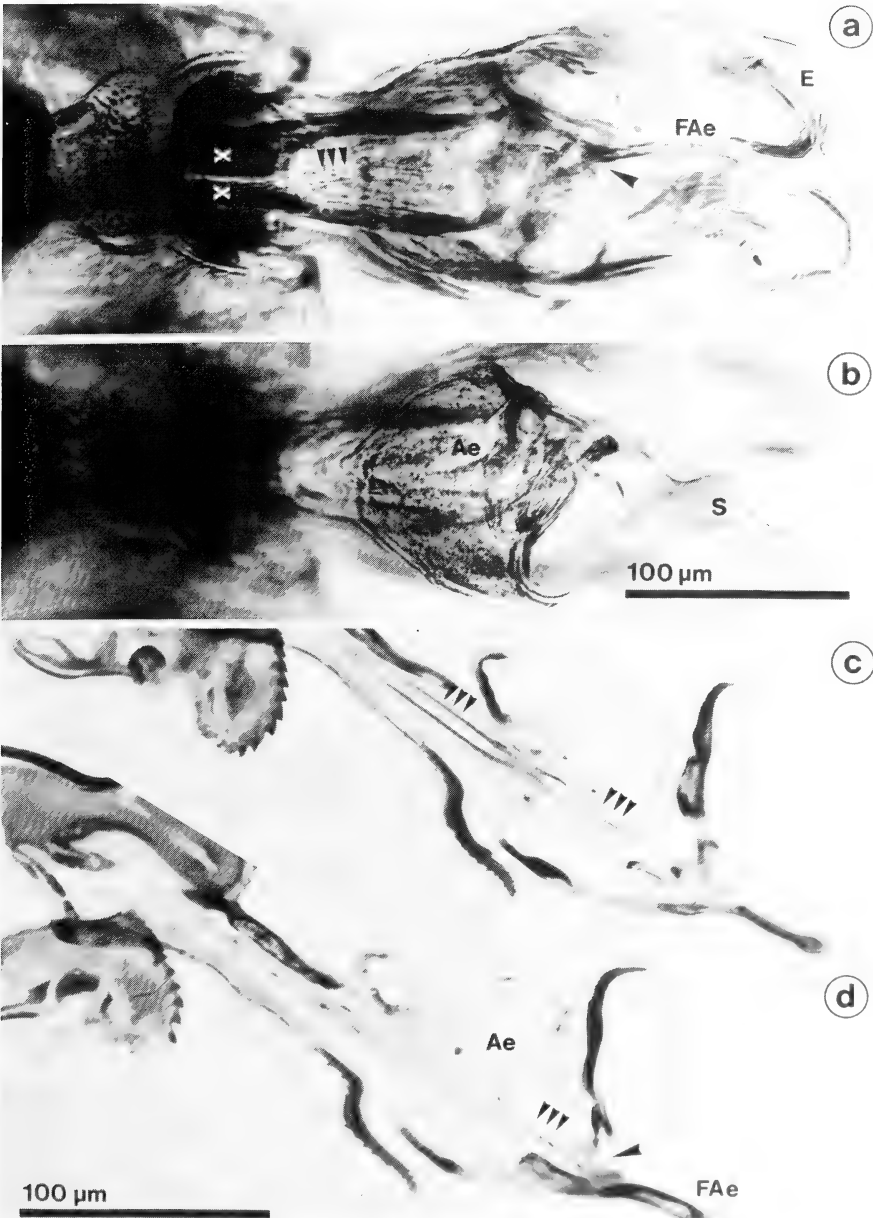
Ae: Aedeagus, E: Epiphallus, FAe: Fortsatz des Aedeagus, S: austretendes Spermatophorenmaterial, gro-
ßer Pfeil: Phallotrema, kleine Pfeile: Ductus ejaculatorius II, weiße Kreuze: asymmetrische Sklerite im
Aedeagus.
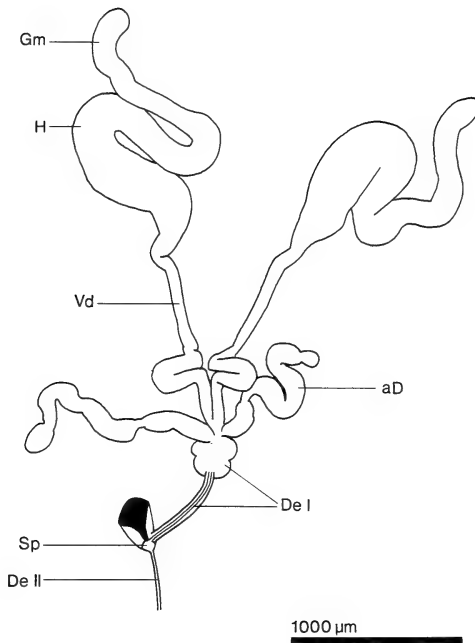
Abb.30: Innere männliche Geschlechtsorgane von *C. whitei*.

aD: akzessorische Drüse, De I+II: Ductus ejaculatorius I und II, Gm: Germarium, H: Hoden, Sp: Spermapumpe, Vd: Vas deferens.

Die Organisation der inneren männlichen Geschlechtsorgane von *C. whitei* entspricht weitgehend den von Kumar (1978 a) beschriebenen Verhältnissen bei *Sphyracephala hearseiana* (Diopsidae).

Die tubulären Hoden von *C. whitei* sind zwei- bis dreimal abgewinkelt. Ihre Wand besteht aus zwei Epithellagen, einem sehr flachen inneren Epithel, dem zum Hämolymphraum hin ein dickeres, braun pigmentiertes Epithel aufgelagert ist. Außerdem enthält die Hodenwand Muskelfasern, die sie im Nativpräparat zu peristaltischen Bewegungen befähigen. Während das distale Ende der Hoden, das Germarium, gleichmäßig dicht mit rundlichen Spermatogonien angefüllt ist, liegen die Zellen weiter proximal in deutlich voneinander abgesetzten Gruppen. Noch weiter proximal enthalten die Hoden unterschiedliche Stadien der Spermiohistogenese, von Spermatocytengruppen bis hin zu individuell beweglichen, fadenförmigen Spermatozoen, die nicht mehr in Bündeln zusammengefaßt sind (Abb.31a).

Nach Snodgrass (1935) bestehen die Hoden der meisten Dipteren nur aus einem einzigen Tubulus. Daß die deutlich voneinander abgesetzten Zellgruppen in den Hoden von *C. whitei* nicht aus getrennten Hodentubuli hervorgehen, folgt auch daraus, daß im Germarium keine solche Unterteilung festzustellen ist. Snodgrass bezeichnet diese Zellgruppen als „spermatogonial groups", da es sich um die Tochterzellen einer Spermatogonie handelt. Bei der dem Hämolymphraum zugewandten, pigmentierten Epithelschicht der Hodenwand handelt es sich nach Snodgrass um ein Peritoneum.

Proximal gehen die Hoden in die Vasa deferentia über, die innen ein relativ hohes, sekretorisches Epithel besitzen und außen von dem gleichen Pigmentepithel wie die

Tab.1: Größe der inneren männlichen Geschlechtsorgane von *C. whitei* und die jeweilige Ausprägung von Epithel und Cuticula.

Organ		Länge	Durchmesser des Lumen	Höhe und Qualität von Epithel und Cuticula
Hoden		2—3 mm	300 μm	1 μm Epithel + 6 μm Pigmentepithel
Vasa deferentia		1,5 mm	35 μm	20 μm sekretor. Epithel + 6 μm Pigmentepithel
akzessor. Drüsen		1,5 mm	120 μm	3 μm Drüsenepithel + 1 μm Plattenepithel
Ductus ejacul. I	Anfangsteil	75 μm	30 μm	100—150 μm Drüsenepithel + Cuticula <1μm
	Rest	600 μm	7 μm	10 μm kubisches Epithel + 2,5 μm Cuticula
Spermapumpe		30 μm	30 μm	1 μm Epithel + 3—15 μm Cuticula
Ductus ejacul. II		400 μm	7 μm	1 μm Epithel + 2 μm Cuticula

Hoden überzogen sind (Abb.31a). Die Endabschnitte der Vasa deferentia verlaufen dicht nebeneinander und sind in diesem Bereich gemeinsam von dem Pigmentepithel umhüllt. Sie vereinen sich, kurz bevor sie durch einen Sphinkter in den erweiterten Anfangsteil des Ductus ejaculatorius I einmünden (Abb.31b). Die Vasa deferentia enthalten Spermatozoen und ca. 0,5—2,0 μm große, mit Toluidinblau stark anfärbbare Sekrettröpfchen, die den Inhalt granulär erscheinen lassen. Die Spermatozoen zeigen im Nativpräparat individuelle wellenförmige Bewegungen.

Die akzessorischen Drüsen sind tubulär. Ihre epitheliale Wandung ist relativ dünn, ihr Inhalt homogen und mit Toluidinblau schwach anfärbbar (Abb.31). Im Gegensatz zu den akzessorischen Drüsen der Weibchen konnte bei denen der Männchen lichtmikroskopisch keine Cuticulaauskleidung gefunden werden. Auch die Vasa deferentia und die akzessorischen Drüsen zeigen im Nativpräparat peristaltische Bewegungen.

Der erweiterte Anfangsteil des Ductus ejaculatorius I ist von einem Polster aus hohen Drüsenzellen mit cuticulären Ausführkanälchen umgeben (Abb.31b). Sein Lumen ist von einer sehr dünnen Cuticula ausgekleidet. Der restliche Gang besitzt hingegen eine Wand aus dicker, netzartig versteifter Cuticula, die einem kubischen Epithel aufliegt. Der Gang ist von einem reich verzweigten Tracheennetz umgeben, Muskulatur ist nicht vorhanden. Infolge der Circumversion ist der Ductus ejaculatorius I einmal um den Hinterdarm gewunden, bevor er in die Spermapumpe mündet.

Die Spermapumpe besteht aus einem runden Hohlkörper aus teilweise sklerotisierter Cuticula („Vesica") und dem cranial daran ansetzenden Ejakulationsapodem (Abb.32a). In die Vesica mündet dorsocranial der Ductus ejaculatorius I über eine Ventilstruktur. Ihr caudaler Ausgang zum Ductus ejaculatorius II ist hingegen glatt und trichterförmig. Zahlreiche Muskelfasern ziehen von der fächerförmigen Muskelansatzfläche des
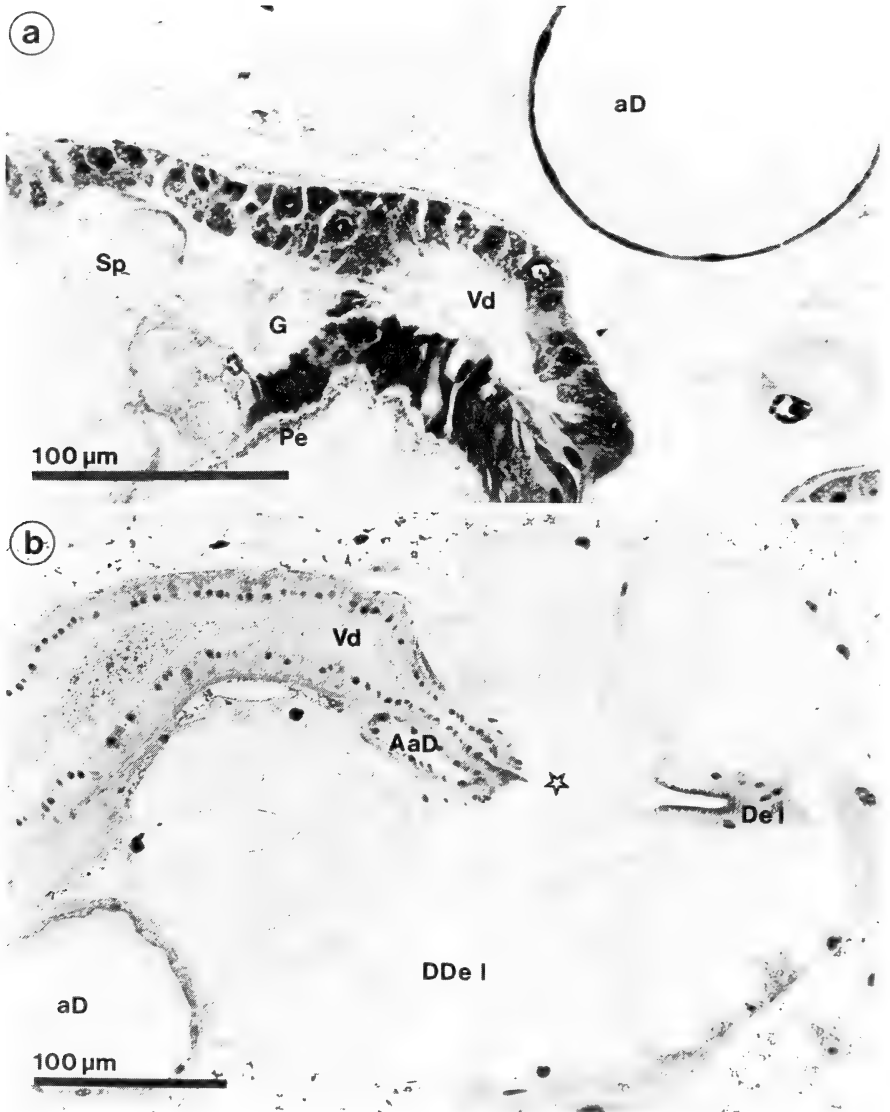
Abb.31: Innere männliche Geschlechtsorgane von *C. whitei*, Semidünnschnitte, Richardson. (a) Übergang vom Hoden zum Vas deferens, akzessorische Drüse; (b) Einmündung von Vasa deferentia und akzessorischen Drüsen in den erweiterten Teil des Ductus ejaculatorius I, der von einem Drüsenpolster umgeben ist.

aD: akzessorische Drüse, AaD: gemeinsame Mündung der beiden akzessorischen Drüsen, DDeI: Drüse am Anfangsteil des Ductus ejaculatorius I, DeI: Ductus ejaculatorius I, G: granuläres Sekret, Pe: Pigmentepithel, Sp: fadenförmige Spermatozoen, Vd: Vas deferens, Stern: erweiterter Anfangsteil des Ductus ejaculatorius I.

Ejakulationsapodem zur caudalen Wandung der Vesica. Bei Kontraktion dieser Muskeln wird der Hohlkörper komprimiert (Abb.32b). Die Ansatzstelle des Ejakulationsapodem an der Vesica ist von Kanälchen durchsetzt, durch die sich Drüsenzellen ins Lumen der Vesica entleeren (Abb.32c—e).

Der Ductus ejaculatorius II besitzt eine glatte Cuticulawand, die einem flachen Epithel aufliegt. Er führt durch den ringförmigen Phallophor und, schmäler werdend, durch den Aedeagus bis zum Phallotrema, das an der Basis des stabförmigen Fortsatzes des Aedeagus liegt (Abb.29c,d).

Der primäre männliche Gonoporus liegt an der Einmündung des Ductus ejaculatorius I in die Spermapumpe (Hennig 1973, Ulrich 1974), die im Zuge der Evolution der Cyclorrhapha nach innen verlagert wurde. Der Ductus ejaculatorius II ist dementsprechend eigentlich als innere Verlängerung des Endophallus („Phallusrohr", Hennig 1973) zu verstehen. Die unterschiedliche Herkunft der beiden Gänge spiegelt sich auch in ihrem histologisch unterschiedlichen Bau wider.

Ektodermale Drüsen im Bereich des Ductus ejaculatorius I sind auch bei anderen Dipteren bekannt. Das Drüsenpolster am Anfangsteil des Ductus ejaculatorius I scheint mit der von Kumar & Nutsugah (1976) abgebildeten Struktur AG2 bei *Diopsis thoracica* („enlarged divergent structure") homolog zu sein. Diese ist jedoch tubulär ausgebildet und relativ zu den restlichen Organen viel größer. Auch bei *Melanagromyza obtusa* (Ipe 1967), *Drosophila melanogaster* (Davey 1985) und *Musca domestica* (Leopold 1971) ist der craniale Teil des Ductus ejaculatorius I sekretorisch differenziert. Die Drüsenzellen an der Basis des Ejakulationsapodem von *C. whitei* sind mit einiger Sicherheit homolog mit der „pressure chamber gland" von *Melanagromyza obtusa* (Ipe 1967), die sich durch einen einzigen, stark chitinisierten Gang an der Basis des Ejakulationsapodem in die Spermapumpe entleert. Bei *Drosophila melanogaster* wird im Epithel der Spermapumpe eine Substanz sezerniert, die bei der Kopulation im Weibchen einen „mating plug" bildet (Bairati & Perotti 1970).

Bei der Bildung der Spermatophore (s. „Spermatransfer") während der Kopulation werden die Inhalte der Vasa deferentia und der akzessorischen Drüsen getrennt abgegeben. Dies ist so vorstellbar, daß sich, während die Spermapumpe in Aktion ist, diese Organe nacheinander kontrahieren und, gesteuert durch Sphinktermuskeln, ihren Inhalt in den Ductus ejaculatorius I abgeben. Das granuläre Sekret der Vasa deferentia mit den beigemischten Spermatozoen scheint den Inhalt der Spermatophore zu bilden, während das homogene Sekret der akzessorischen Drüsen am Aufbau der Spermatophorenwand beteiligt ist. Die Sekrete der ektodermalen Drüsenzellen am Anfang des Ductus ejaculatorius I und an der Basis des Ejakulationsapodem könnten ebenfalls am Aufbau der Spermatophorenwand beteiligt sein (beispielsweise als festigende Komponente), zur Ernährung oder Aktivierung der Spermatozoen beitragen, als Nährstoffe für das Weibchen bestimmt sein oder das Kopulations- bzw. Eiablageverhalten der Weibchen beeinflussen (Leopold 1976, Gillott & Friedel 1977, Gromko 1984, Davey 1985). Aufschluß über die Funktion dieser Sekrete werden erst histochemische und autoradiographische Methoden erbringen.

Spermatozoen

Die Spermatozoen von *C. whitei* sind fadenförmig und ca. 178 μm lang ($\pm 9 \mu$m; n = 30) (Abb.33a). Dem zugespitzten Vorderende folgt ein 0,35—0,50 μm dicker Hauptteil, der etwa 2/3 der Gesamtlänge einnimmt (122$\pm$9 μm; n = 21), und ein nur 0,13—0,20 μm dicker Endteil (Länge 52$\pm$7 μm; n = 13).
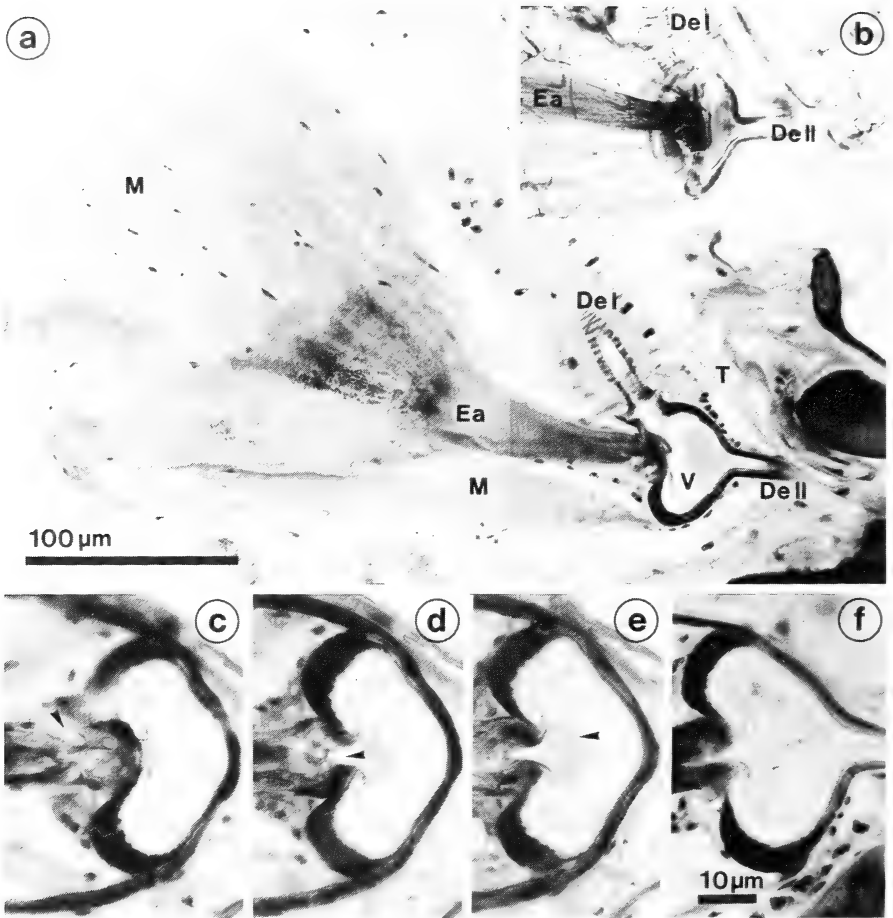
Abb.32: Spermapumpe von *C. whitei*. (a) medianer Semidünnschnitt, Richardson, nach 40 s Kopulation fixiert (Vesica, Ductus ejaculatorius I und II enthalten Sekret der akzessorischen Drüsen); (b) Lateralansicht eines Totalpräparates von links in gleicher Vergrößerung, Vesica komprimiert; (c—e) frontale Semidünnschnitte, Richardson, nach 15 s Kopulation fixiert (aus Drüsen an der Basis des Ejakulationsapodem tritt Sekret aus); (f) frontaler Semidünnschnitt, Richardson, nach 40 s Kopulation fixiert (Vesica enthält Gemisch aus akzessorischen Sekreten und Spermatozoen); Die Vergrößerung in (c—f) ist gleich.

De I + II: Ductus ejaculatorius I und II, Ea: Ejakulationsapodem, M: Muskulatur vom Ejakulationsapodem zur Basis der Vesica, T: Trachee, V: Vesica, Pfeil: Drüsen an der Basis des Ejakulationsapodems und austretendes Sekret.

Der Hauptteil (Abb.33d,e, 39b) enthält ein radiär strukturiertes Axonem von ca. 0,2 μm Durchmesser und zwei im Querschitt ovale Mitochondrienderivate, die eine parakristalline Struktur aufweisen. Zwischen den Mitochondrienderivaten liegt ein bandförmiger Anschnitt, bei dem es sich um den Kern handeln dürfte. In einigen Querschnitten wurden darüberhinaus zwei laterale akzessorische Körper gefunden. Der Endteil besitzt einen runden Querschnitt und erscheint im TEM homogen elektronenhell (Abb.33d, e).

Der Hauptteil gleicht im Querschnitt weitgehend der hinteren Kernregion von Simuliidenspermatozoen (Baccetti et al. 1974). Die parakristalline Struktur der Mitochondrienderivate ist bei höheren Dipteren die Regel (Jamieson 1987). Da der Hauptteil der Spermatozoen von *C. whitei* äußerlich keine Gliederung erkennen läßt (Abb.33a), kann die Länge der Kernregion nicht angegeben werden.

Die Standardabweichung der Spermatozoengesamtlänge bei *C. whitei* beträgt ca. 5% des Mittelwertes. Eine Polymegalie, also das Auftreten verschiedener Größenklassen, wie sie für einige Drosophilaarten beschrieben ist (Beatty & Burgoyne 1971), wurde nicht festgestellt.
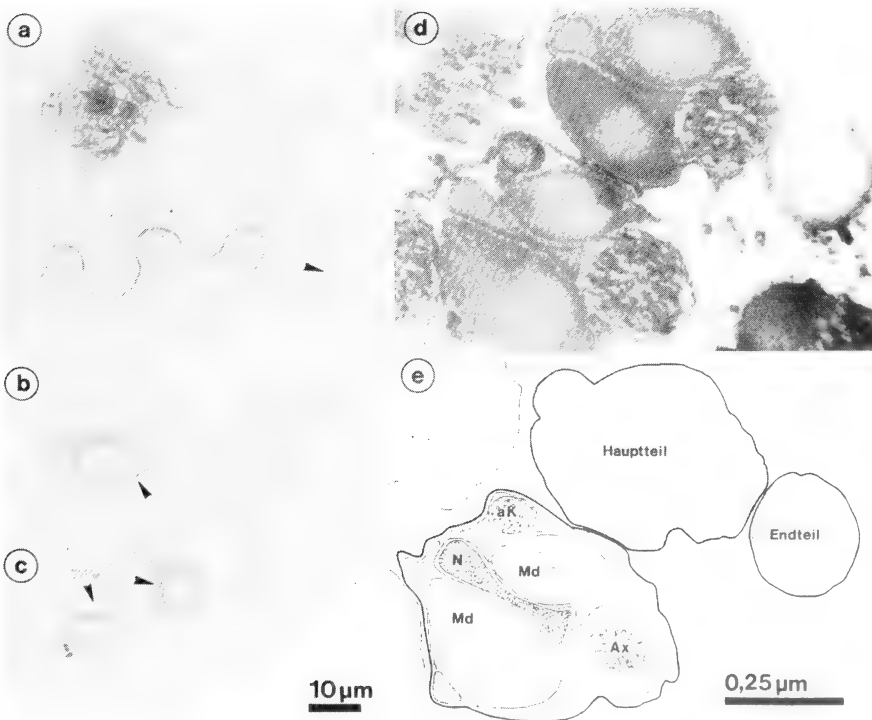
Abb.33: Spermatozoen von *C. whitei*. (a—c) Ausstrichpräparat, Hämatoxilin-Fuchsin, der Pfeil markiert den Übergang zwischen Hauptteil und Endteil; (d) Ultradünnschnitt, TEM, es sind Anschnitte aus dem Hauptteil- und Endteilbereich sichtbar; (e) Schemazeichnung nach (d).

aK: akzessorischer Körper, Ax: Axonem, Md: Mitochondrienderivat, N: Nucleus.

Sich bewegende Spermatozoen können bei geschlechtsreifen Männchen im proximalen Teil der Hoden und in den Vasa deferentia, bei begatteten Weibchen in den Spermatheken und in geringerer Anzahl in den Kammern des ventralen Receptaculum gefunden werden. In Zupfpräparaten in Insektenringer zeigen die Spermatozoen eine dreidimensional wellenförmige Bewegung, aus der jedoch keine erkennbare Vorwärtsbewegung resultiert. Werden diese Präparate durch Lufttrocknen fixiert, so findet man die Hauptteile der Spermatozoen in großen Wellen mit variabler Amplitude von 4,5—13 μm und einer Wellenlänge von ca. 30 μm fixiert, während die Endteile entweder relativ gerade oder in viel kürzeren und flacheren Wellen liegen (Abb.33a).

Ein abweichendes Verhalten wurde in Zupfpräparaten in aqua dest. beobachtet. Viele Spermatozoen liegen hier zunächst in zirkulierenden Rollen von 6,6—9,2 μm Durchmesser vor (8,0±0,8 μm; n=18), ähnlich aufgerollten Schiffstauen, wobei die Endstücke teilweise aus den Rollen heraushängen (Abb.33b,c). Nach einigen Minuten schnellen die Spermatozoen wie durch einen Sprungfedermechanismus in die oben beschriebene Wellenform. Diese schlagartige Streckung erweckt beim Beobachter den Eindruck, als ob dabei potentielle Energie freigesetzt würde.

In Nativpräparaten frisch begatteter Weibchen unter Insektenringer wurden beide Bewegungsformen beobachtet. Spermatozoen in den Spermathekengängen zeigten eine wellenförmige Bewegung, deren Amplitude allerdings durch den geringen Durchmesser des Ganglumens (ca. 5,5 μm) eingeschränkt war. Innerhalb der Spermatophoren konnten Spermatozoenrollen beobachtet werden, hier mit einem Durchmesser von 10,5—14,5 μm (11,3±1,8 μm; n=8).

Sowohl Wellen- als auch Rollenform der Spermatozoen von *C. whitei* konnten im Nativpräparat innerhalb der weiblichen Geschlechtsorgane beobachtet werden. Es handelt sich also um zwei natürlich vorkommende Bewegungsformen, die wahrscheinlich durch verschiedene Außenmedien induziert werden. Nach Baccetti & Afzelius (1976) werden Geschwindigkeit und Form der Bewegung von Insektenspermatozoen unter anderem durch Osmolarität, pH und Ionengehalt des umgebenden Milieus beeinflußt. Da der Übergang zwischen den beiden Bewegungsformen in Sekundenbruchteilen erfolgt, muß bei allen fixierten Präparaten eine auf die Präparation bzw. Fixierung zurückgehende, veränderte Lage der Spermatozoen in Erwägung gezogen werden.

Die dreidimensionale Wellenbewegung der Spermatozoen von *C. whitei* entspricht in ihrer Größenordnung etwa der „secondary wave" bei *Megaselia scalaris* (Curtis & Benner 1991), bzw. der „helicalen Welle" bei *Aedes aegypti* (Linley & Simmons 1981c) und bei *Tenebrio molitor* (Baccetti & Afzelius 1976). Eine überlagerte, kürzere Welle, wie sie bei den genannten Arten beschrieben wurde, konnte bei *C. whitei* mit den bisher angewandten Methoden nicht eindeutig nachgewiesen werden.

Die Rollenform stellt möglicherweise eine Speicherform dar. In den Cuticulakammern des ventralen Receptaculum (Durchmesser 6,7—7,5 μm, Länge ca. 12 μm) können überhaupt nur eng aufgerollte Spermatozoen (Durchmesser ≧6,6 μm) Platz finden. Auch bei *Megaselia scalaris* können die Spermatozoen einen ringförmigen Zustand annehmen, der, möglicherweise infolge eines reduzierten Energieverbrauchs, wesentlich länger beweglich bleibt als die gestreckte Form (Curtis & Benner 1991). Lensky & Schindler (1967) beschreiben in einer Arbeit über Bienenspermatozoen ebenfalls eine zirkulierende Rollenform, die in eine „schlangenartige" Form übergeht.

An frei in Insektenringer schwimmenden Spermatozoen von *C. whitei* wurde eine aktive Fortbewegung nicht beobachtet. Es ist aber nicht auszuschließen, daß die schraubig-schlängelnde Bewe-

gungsweise der Spermatozoen gerade in den engen Lumina der Spermathekengänge oder zwischen den Cuticulaborsten im Eingang des ventralen Receptaculum doch einen Vortrieb erzeugt. Wenn auch einige Autoren die Fähigkeit von Insektenspermatozoen zur aktiven Fortbewegung für relativ unbedeutend halten (DeVries 1964, Hinton 1964, Davey 1965, Khan & Musgrave 1969, Linley & Simmons 1981c), so gibt es doch mehrere Beispiele, bei denen eine aktive, möglicherweise chemo-taktische Fortbewegung beobachtet wurde (Nonidez 1920, Ruttner & Koeniger 1971, Gessner & Ruttner 1977, Davey 1985, Curtis & Benner 1991). Curtis & Benner (1991) haben darüberhinaus nachgewiesen, daß die Fortbewegung von Phoriden-Spermatozoen wesentlich beschleunigt werden kann, wenn die Viskosität des Mediums durch Zugabe von Methylcellulose erhöht wird. Es wäre denkbar, daß die filamentöse Substanz, die in den Kammern des ventralen Receptaculum und in den Spermatheken von *C. whitei* gefunden wurde, eine derartige Funktion erfüllt.
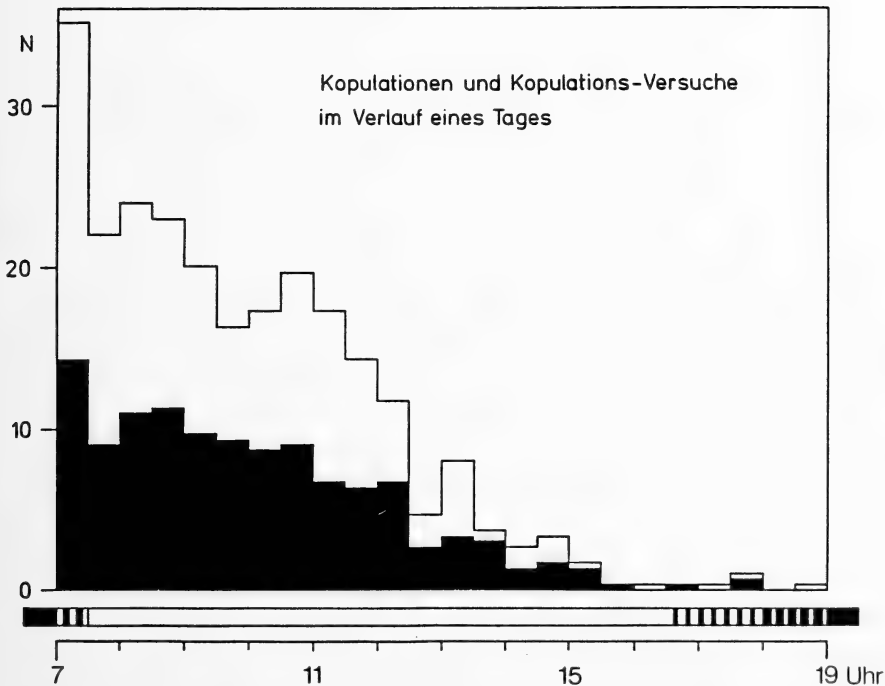
Abb.34: Verlauf der Kopulationsaktivität von *C. whitei* in einer Population aus 7 Weibchen und 5 Männ-chen während eines Tages.

Abszisse: Zeit in 30-Minuten-Intervallen von Tagesanfang bis Tagesende; der Balken unter dem Dia-gramm zeigt die Beleuchtungsverhältnisse (Nacht/Dämmerung/heller Tag); Ordinate: Mittlere Zahl der Kopulationen (schwarz) und Kopulationsversuche unter 30 s (weiß) pro Zeitintervall und Tag. Die schwarzen und weißen Balken sind aufeinandergesetzt und überschneiden sich nicht.

REPRODUKTIONSGESCHEHEN

Kopulation

Unter Laborbedingungen wird *C. whitei* ca. 12 Tage nach dem Schlüpfen geschlechts-reif. Danach kopulieren sowohl Männchen als auch Weibchen in der Regel mehrmals täglich, besonders häufig in den Morgenstunden (Abb.34). Beide Geschlechter sind pro-miskuitiv.

In Laborversuchen mit gemischten Populationen kopulierten Weibchen im Mittel 17 mal (±10; n=21), maximal 34 mal pro Tag. Bei den Männchen betrug die tägliche Kopulationsrate im Mittel 23 (±11; n=15), maximal 37. Sowohl Männchen als auch Weibchen kopulierten oft in schneller Folge hintereinander mit verschiedenen Partnern (Abb.35). Die individuellen Schwankungen in der Kopulationsaktivität von Tag zu Tag ließen innerhalb eines Beobachtungszeitraumes von 14 Tagen keine Periodizität erken-nen. Im natürlichen Habitat (Malaysia) wurde ein Weibchen beobachtet, das innerhalb von 3 Stunden 26 mal kopulierte.

Verhalten bei der Kopulation

Die ersten Kopulationen am Tag finden oft schon morgens am Schlaffaden statt. Später verteidigen besonders größere Männchen häufig temporäre Territorien an zur Nah-
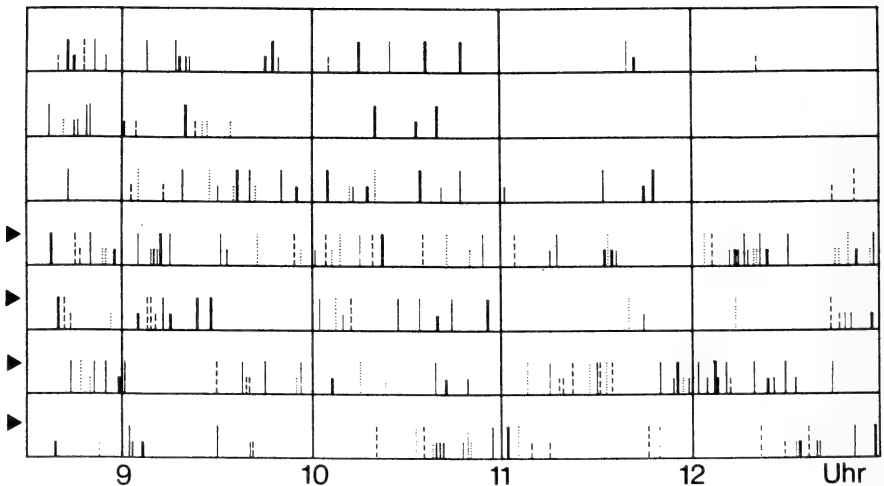
Abb.35: Originaldaten aus der Beobachtung einer Population aus 7 Weibchen (verschiedene Zeilen) und 5 Männchen (verschiedene Strichmuster).

Abszisse: Uhrzeit; lange Striche: Kopulationen; kurze Striche: Kopulationsversuche unter 30 s; die mit einem Pfeil gekennzeichneten Weibchen kopulierten im Beobachtungszeitraum mit allen vorhandenen Männchen.

rungsaufnahme oder Eiablage geeigneten Stellen und kopulieren mit ankommenden Weibchen. Aber auch bei „Zufallsbegegnungen" wird gelegentlich kopuliert.

Der Kopulation geht kein erkennbares Balzverhalten voraus. In der Regel versuchen die Männchen, nachdem sie ein Weibchen mehr oder weniger lange fixiert haben, unvermittelt auf dessen Rücken aufzuspringen. Da dieser Sprung aus verschiedensten Richtungen erfolgen kann, hat das Männchen oft zunächst Mühe, auf dem Weibchen Halt zu finden und seinen Körper parallel zu dem des Weibchens zu orientieren. Anschließend krümmt das Männchen sein Abdomen hinter dem Weibchen nach unten und streift in einer darauffolgenden Aufwärtsbewegung mit seinen ausgestreckten Genitalien an denen des Weibchens entlang. Häufig streckt das Weibchen sein Abdomenende lang aus und spreizt die Cerci nach hinten ab. Gelingt die Kopulation nicht schon beim ersten Kontakt der Genitalien, so wiederholt das Männchen seine Abdomenbewegungen, wobei das Streifen der weiblichen Genitalien in ein intensiveres Befühlen übergehen kann. Bei Nichtgelingen können die Kopulationsversuche über mehrere Minuten fortgesetzt werden.

Die letzte Entscheidung darüber, inwieweit die Kopulation vollzogen wird, fällt wahrscheinlich erst während des Genitalkontaktes. Chemorezeptoren könnten in dieser Phase Informationen über Reifegrad der Gameten, Ernährungs- oder Gesundheitszustand des Partners erhalten, aber auch an Kontaktpheromone ist in diesem Zusammenhang zu denken.

Das Weibchen kann durch Abspreizen seiner Cerci den Genitalkontakt erleichtern. Gleichzeitig exponiert es dadurch die Setae auf seiner Subanalplatte, deren Reizung ein reflexartiges Hervorstülpen der Vagina bewirkt (s. „äußere Merkmale des weiblichen Abdomens"). Dieses Hervorstülpen der Vagina könnte seinerseits eine notwendige Voraussetzung für das Eindringen des männlichen Kopulationsapparates darstellen.

Ein aktives Hervorstülpen der Vagina bei der Kopulation ist auch für *Calliphora erythrocephala* (Graham-Smith 1938) und *Musca domestica* (Degrugillier & Leopold 1973) beschrieben worden (Diskussion 2.3). Aber auch *Aedes aegypti* stülpt bei der Kopulation einen Teil der inneren weiblichen Geschlechtsorgane hervor (Spielmann 1964).

Nachdem der männliche Kopulationsapparat in die Vagina des Weibchens eingeführt ist, verharrt das Paar relativ ruhig. Pumpbewegungen des Männchens konnten nicht beobachtet werden. Im Labor betrug die Kopulationsdauer tagsüber, bei einer Temperatur von ca. 27 °C, im Mittel 45 s (±6 s; n=169), in der mit ca. 24 °C etwas kühleren Morgendämmerung im Mittel 53 s (±9 s; n=190). Die längste beobachtete Kopulation dauerte 80 s.

Der Unterschied zwischen den Kopulationsdauern morgens und tagsüber läßt sich mit dem t-Test zur 0,1%-Grenze sichern. Er hängt möglicherweise mit den genannten Temperaturunterschieden zusammen ($Q_{10}=1,76$).

Nach der Kopulation trennen sich die Partner abrupt, bleiben aber meist noch relativ nahe beieinander, wobei sie sich putzen oder Nahrung aufnehmen. Häufig erfolgt nach einiger Zeit eine erneute Kopulation. Es kommt auch vor, daß eine Kopulation nach weniger als 30 s beendet wird. Aus solchen Kopulationen gehen aber in der Regel keine Nachkommen hervor (de la Motte, mündliche Mitteilung), was dafür spricht, daß in solchen Fällen kein Sperma übertragen wird.

66

Lage der Genitalien während der Kopulation

Um die Lage der männlichen Geschlechtsorgane im Genitaltrakt der Weibchen zu ermitteln, wurden Paare während der Kopulation in flüssigem Stickstoff fixiert. In solchen Präparaten ist die Vagina des Weibchens beträchtlich caudad verlagert, ihr Ende ist etwas aus der Vulva herausgestülpt. Die aktuelle Hinterkante der Vagina wird durch das nach ventral umgebogene Ende des sklerotisierten Ringes gestützt (Abb.36). Die Genitalpapille wird im Zuge dieser Verschiebung so verformt, daß die Öffnung der Spermathekengänge nach caudal weist.

Der männliche Kopulationsapparat wird so weit in die Vagina eingeführt, daß der von den Postgoniten gebildete Kragen mit der Vulva abschließt. Die Schaufeln des Epiphallus kommen an der ventralen Wand der Vagina in der Nähe des sklerotisierten Ringes zu liegen, während der Fortsatz des Aedeagus mit seinem Endhaken in die Öffnung der Spermathekengänge eindringt (Abb.36).

Eine oberflächliche Betrachtung dieser Lagebeziehungen könnte leicht zu der Annahme führen, daß das Sperma durch den Fortsatz des Aedeagus direkt in die Spermathekengänge injiziert wird. Tatsächlich liegt das Phallotrema jedoch an der Basis dieses Fortsatzes und der Spermatransfer erfolgt mit Hilfe einer Spermatophore. Das Einhaken des Aedeagus in die Mündung der Sperma-
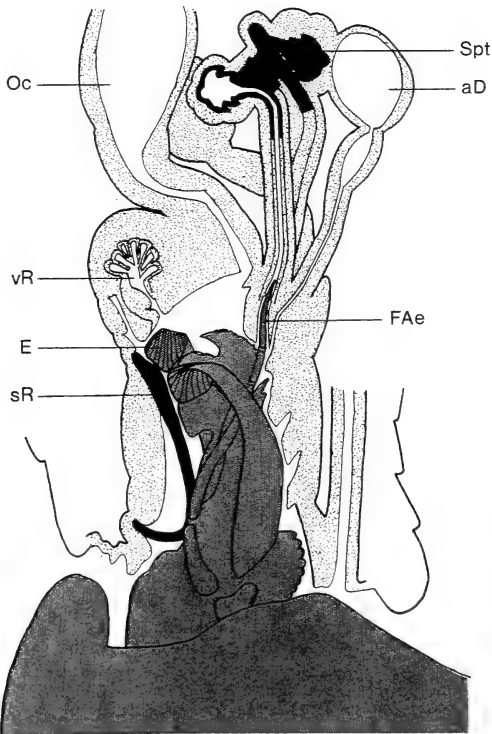
Abb.36: Innere weibliche und äußere männliche Geschlechtsorgane von *C. whitei* in Kopulationsstellung, Lateralansicht von links. Weibchen oben, innere Geschlechtsorgane gepunktet; Männchen unten, schattiert.

aD: akzessorische Drüse, E: Epiphallus, FAe: Fortsatz des Aedeagus, Oc: Oviductus communis, Spt: Spermathek, sR: sklerotisierter Ring, vR: ventrales Receptaculum.

thekengänge dient wahrscheinlich der exakten Positionierung der männlichen Geschlechtsorgane in der Vagina. Möglicherweise wird der Endhaken auch eingesetzt, um die Mündung der Spermathekengänge aufzuhebeln, so daß der Spermatophorenhals eindringen kann. Auch bei *Glossina austeni* (Pollock 1974) und bei *Culicoides melleus* (Linley 1981a), die beide ebenfalls Spermatophoren verwenden, wird die Spitze des Aedeagus in die Mündung der Spermathekengänge eingeführt, möglicherweise um diese aufzuspreizen.

Die hakenförmig gebogenen Schaufeln des Epiphallus scheinen an der cranialen Rundung des sklerotisierten Ringes Halt zu finden, und so ebenfalls zur Positionierung bzw. Fixierung der männlichen Geschlechtsorgane beizutragen. Möglicherweise sind sie auch an der Formung der Spermatophore beteiligt (s. „Spermatransfer mittels Spermatophore"). Nach seiner Form und Lage wäre der Epiphallus prinzipiell geeignet, eine bereits vorhandene Spermatophore zu displazieren oder aus der Vagina zu entfernen. Ein derartiger Mechanismus wurde bei Odonaten beschrieben (Waage 1979). Abgesehen von dem Befund, daß nie zwei Spermatophoren in einem Weibchen gefunden wurden, gibt es jedoch bei *C. whitei* für eine derartige Funktion bisher keine Evidenzen.

Spermatransfer mittels Spermatophore

Während der nur ca. 45 s dauernden Kopulation produziert das Männchen innerhalb der Vagina des Weibchens eine Spermatophore. Diese besitzt eine einzige Spermakammer, aus der Spermatozoen und akzessorische Sekrete über ein Halsstück in die Mündung der Spermathekengänge entleert werden. Einige Zeit nach der Kopulation wird die Hülle der Spermatophore vom Weibchen ausgeschieden.

Die Spermatophore von *C. whitei* ist die erste, die bei acalyptraten Fliegen nachgewiesen wurde (Kotrba 1990). In der Ordnung Diptera waren Spermatophoren bisher nur in einigen Familien der Nematocera (Ceratopogonidae (Pomeranzew 1932), Chironomidae (Nielsen 1959), Simuliidae (Rubzow 1959), Bibionidae (Leppla et al. 1975)) und in einer einzigen Gattung der calyptraten Brachycera (*Glossina*, Pollock 1970) bekannt. Eine vergleichende Zusammenstellung der Spermatophorenmerkmale der verschiedenen Dipterenfamilien ist in Tabelle 4 und Abb.46 zu finden.

In der vorliegenden Arbeit wird der Begriff „Spermatophore" gemäß der Definition von Weber (1933) verwendet: „Die Spermatophoren sind Spermien- oder Spermiozeugmenmassen, die durch Hüllen zusammengehalten werden. Die Hüllen werden an der Mündung der männlichen Geschlechtswege aus dem Sekret der Anhangsdrüsen derselben gebildet und erlangen ihre endgültige Form entweder schon vor der Übertragung oder erst nach der Übertragung. Im letzteren Fall passen sich die Spermatophoren aufs engste an die Form des Teils der weiblichen Geschlechtswege an, der sie aufnimmt." Es muß betont werden, daß der Begriff „Spermatophore" an sich mit keiner Aussage über die Homologie dieser Strukturen verknüpft ist.

Morphologie der Spermatophore

Die Spermakammer ist keulenförmig und leicht spiralig gewunden (Abb.38a—d). Sie ist im Mittel 93 μm lang ($\pm$11 μm; n=21) und hat an ihrem dicken Ende einen mittleren Durchmesser von 48 μm ($\pm$5 μm; n=22). Zum anderen Ende hin verjüngt sie sich und mündet durch eine Engstelle in den Spermatophorenhals. Der Hals ist ca. 9 μm dick ($\pm$2 μm; n=9) und ca. 41 μm lang ($\pm$4 μm; n=8).

Die Wand der Spermatophore besteht aus mehreren Schichten unterschiedlicher Dichte (Abb.39b) und Anfärbbarkeit. An der Innenseite liegt eine ca. 0,2 µm dicke Lage aus elektronendichtem Material (L I). Nach außen hin schließt sich weniger elektronendichtes Material an, das eine Schichtung parallel zur Oberfläche aufweist (L II). Zusammen sind diese beiden Schichten in den verschiedenen Bereichen der Spermatophorenwand 0,5—3,0 µm dick. Nur stellenweise an die Oberfläche von Spermakammer und Spermatophorenhals angeheftet, umgibt eine weitere Schicht aus schwammigem Material (L III) die Spermatophore wie ein Trichter oder wie das Einschlagpapier einen Blumenstrauß (Abb.38c, 39a).

Das Material der Spermatophorenwand läßt sich mit basischem Fuchsin und Toluidinblau anfärben, und zwar umso stärker, je elektronendichter es ist. In Direkttiefschwarz färbt sich die Wand der Spermakammer dunkelgrau, während der Hals und das schwammige Material nur schwach angefärbt werden (Abb.38d). Die Spermakammer ist außerdem relativ KOH-resistent.

Die Wand der Spermatophore von *Glossina morsitans* besteht aus einem Gemisch aus Proteinen und Kohlenhydraten (Odhiambo et al. 1983, Kokwaro et al. 1987). Auf eine ähnliche Beschaffenheit scheinen die chemischen Eigenschaften der Spermatophorenwand von *C. whitei* hinzuweisen. Direkttiefschwarz färbt Polysaccharide wie Baumwolle (Zellulose) und Chitin besonders stark. Die intensive Anfärbung der Spermakammer in Direkttiefschwarz, sowie ihre relativ hohe KOH-Resistenz könnte auf die Anwesenheit ähnlicher Polysaccharide hinweisen. Hier ist jedoch ohne histochemische Nachweisverfahren keine gesicherte Aussage möglich.

Inhalt der Spermatophore

Der Inhalt der Spermatophore besteht aus einer Suspension aus fadenförmigen Spermatozoen und runden Tröpfchen, die locker in einer Flüsigkeit verteilt liegen. Er erinnert an den Inhalt der männlichen Vasa deferentia (s. „Innere männliche Geschlechtsorgane").

Die Spermatozoen liegen in der Spermakammer locker verteilt. Im Nativpräparat erkennt man aufgerollte Spermatozoen in der Spermakammer, in Schnittpräparaten hingegen ist keine gerichtete Anordnung erkennbar (Abb.38e, 39a).

In den Spermatophoren der Dipteren *Glyptotendipes paripes* (Nielsen 1959), *Culicoides melleus* (Linley 1981a), *Simulium salopiense* (Davies 1965) und *Dilophus febrilis* (Abb.46) sind die Spermatozoen in parallelen Bündeln gelagert (Tab.4). Im Vergleich dazu stellt die lockere Anordnung der z.T. rollenförmigen Spermatozoen in der Spermatophore von *C. whitei* eher eine Ausnahme dar. Im Stadium der Entleerung wurden jedoch auch in der Spermatophore von *Culicoides melleus* aufgerollte Spermatozoen beobachtet (Linley & Adams 1971). Ob Leppla et al. (1975) in der Spermatophore von *Plecia nearctica* aufgerollte Spermatozoen beobachteten, ist ungewiß. Sie schreiben: „Granular spermatozoa from the gelatinous spermatophore network become motile and traverse the system."

Die zahlreichen Tröpfchen von 0,5—2,0 µm Durchmesser geben dem Spermatophoreninhalt im Nativpräparat ein granuläres Aussehen (Abb.38a,e, 39a). Sie bestehen aus einem homogenen, sehr elektronendichten Material, das mit Toluidinblau und basischem Fuchsin stark anfärbbar ist.

Granuläre Bestandteile sind auch dem Sperma anderer Dipteren beigemengt (*Culicoides melleus* (Linley 1981a), *Glyptotendipes paripes* (Leppla et al. 1975), *Simulium salopiense* (Davies 1965), *Drosophila melanogaster* (Nonidez 1920), *Aedes aegypti* (Spielman 1964)). Ihre Funktion ist noch nicht geklärt. Möglicherweise enthalten die elektronendichten Tröpfchen in der Spermatophore von *C. whitei* eine Art „Proviant" für die wochenlange Speicherung der Spermatozoen im Weib-chen, oder sie tragen zur Ernährung des Weibchens bei (Thornhill 1976b).

Bildung der Spermatophore

Um die Vorgänge bei der Bildung der Spermatophore zu erfassen, wurden Paare wäh-rend der Kopulation in flüssigem Stickstoff fixiert und anschließend zu Schnittserien verarbeitet. Ein nach 15 s fixiertes Präparat zeigt den Austritt eines homogenen Sekrets aus den Drüsenkanälchen in der Basis des Ejakulationsapodem in das Lumen der Vesica (Abb.32c—e). In einem nach 40 s fixierten Präparat findet sich im Ductus ejacu-latorius I und II und in der Spermapumpe des Männchens ein schwach anfärbbares, homogenes Sekret (Abb.32a), dessen Übertritt durch das Phallotrema in das Weibchen sich anhand der Schnittserie verfolgen läßt. Im Weibchen kleidet das Sekret den crania-len Teil der Vagina aus, so daß die Mündungen von Oviductus communis, ventralem Receptaculum und Genitalpapille verdeckt sind. In einer weiteren, ebenfalls nach 40 s fixierten Schnittserie enthalten die Ausführgänge des Männchens ein Gemisch aus
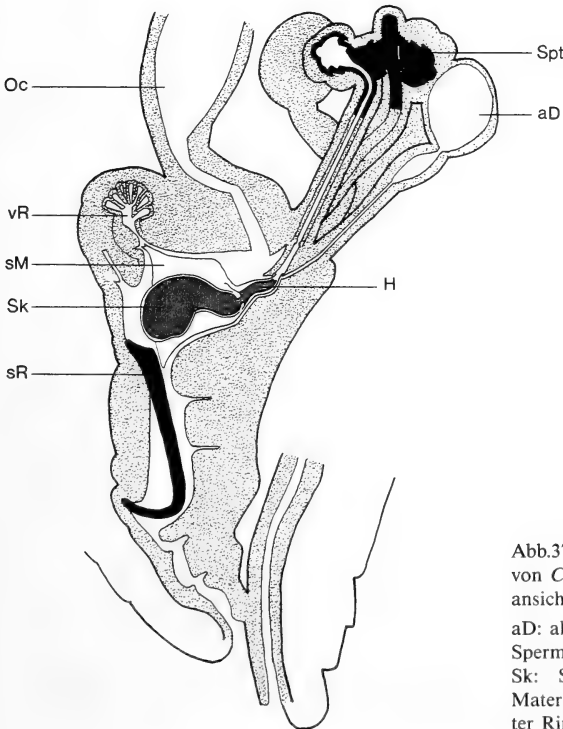
Abb.37: Innere weibliche Geschlechtsorgane von *C. whitei* mit Spermatophore, Lateral-ansicht von links.

aD: akzessorische Drüse, H: Halsstück der Spermatophore, Oc: Oviductus communis, Sk: Spermakammer, sM: schwammiges Material, Spt: Spermathek, sR: sklerotisier-ter Ring, vR: ventrales Receptaculum.

a) Spg, Oc, vR, H, S, sR — 100 µm

b) H, S, sR — 100 µm

c) sM, H, S — 100 µm

d) — 100 µm

e) — 10 µm
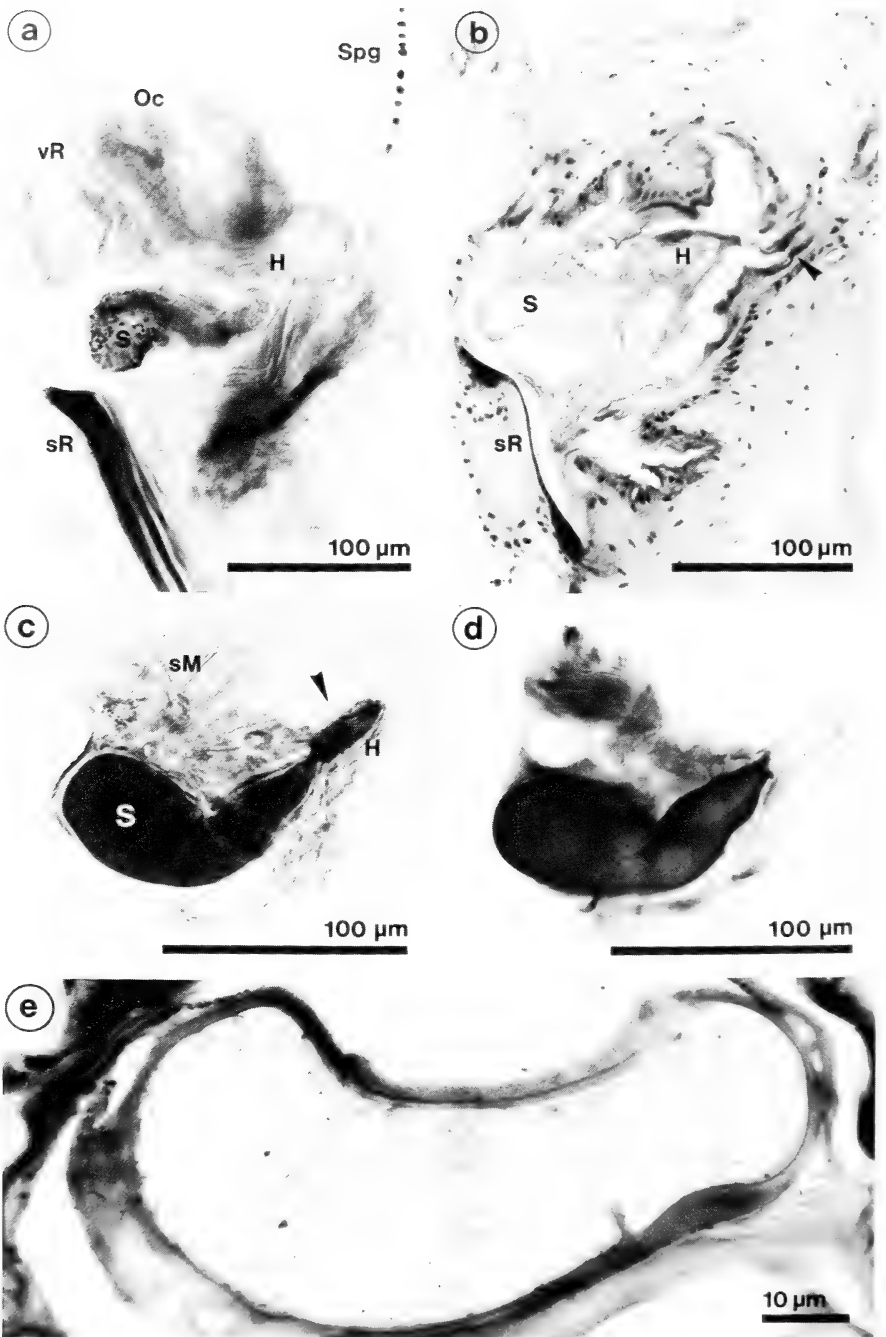
Spermatozoen und Granula (Abb.32f), das auch in der innerhalb der weiblichen Vagina bereits weitgehend ausgeformten Spermatophore zu finden ist, die Spermathekengänge des Weibchens sind aber noch leer.

Bei Weibchen, die direkt nach Beendigung der Kopulation fixiert wurden, findet man die fertige Spermatophore im cranialen Teil der Vagina, wo sie eine charakteristische dorsoventrale Lage einnimmt (Abb.37, 38a). Während das breite Ende der Spermakammer nahe dem cranialen Ende des sklerotisierten Ringes liegt, steckt der Spermatophorenhals in der Mündung der Spermathekengänge. Die äußerste, schwammige Schicht der Spermatophore kleidet den cranialen Bereich der Vagina aus und überdeckt die Mündungen von Ovidukt und ventralem Receptaculum. Den Spermatophorenhals umgibt sie trichterfömig und folgt ihm in die Genitalpapille hinein, wo sie an der Öffnung der Spermathekengänge endet. Das Lumen des Spermatophorenhalses kommuniziert mit dem der Spermathekengänge.

In einigen Fällen wurden ansonsten normal geformte Spermatophoren gefunden, deren Hals vor der Mündung der Spermathekengänge umgebogen war, so daß ein großer Teil der Spermatozoen und des granulären Materials in die Vagina geströmt war (Abb.38b).

Die Spermatophorenbildung bei *C. whitei* entspricht etwa der „first female-determined method" von Gerber (1970). Danach werden männliche Drüsensekrete in einer bestimmten Reihenfolge vor (oder nach) dem Spermatransfer in die Vagina ejakuliert, wo sie die Spermatozoen einkapseln. Die Spermatophore hat eine feste Form, die von der Form der weiblichen Geschlechtswege bestimmt wird (letzteres trifft bei *C. whitei* zumindest für die äußere Spermatophorenhülle aus schwammigem Material zu).

Aus den bisherigen Befunden läßt sich folgender Ablauf der Spermatophorenbildung als plausibel annehmen: Zunächst wird der craniale Teil der Vagina mit dem schwammigen Material ausgekleidet, der späteren äußersten Schicht der Spermatophore. Dabei werden die Öffnungen von Ovidukt, ventralem Receptaculum und Genitalpapille überdeckt. Möglicherweise dringt der Fortsatz des Aedeagus erst danach in die Mündung der Spermathekengänge ein und durchstößt dabei die erste Schicht, die dadurch ihre Trichterform erhält. Aus dem Phallotrema an der Basis des Fortsatzes tritt jetzt tropfenförmig das dichte Material für die Spermakammerwand aus. Als nächstes wird eine Spermatozoen und granuläres Material enthaltende Suspension in das dichte Material eingespritzt, wodurch dieses wie ein Ballon zur Spermakammer ausgedehnt wird. Dort, wo die Spermakammer mit dem schwammigen Material in Kontakt kommt, verkleben die Schichten. Die spiralige Form der Spermakammer könnte durch Unregelmäßigkeiten beim Ausströmen des Materials entstehen, möglicherweise sind auch die Epiphallusschaufeln an ihrer Formung beteiligt.

◀——————————————————————————————————————

Abb.38: Spermatophore von *C. whitei*. (a) Vagina mit Spermatophore, Totalpräparat in Lateralansicht von links, Toluidinblau; (b) Vagina mit Spermatophore mit umgebogenem Spermatophorenhals, medianer Semidünnschnitt, Hämatoxilin-Fuchsin, Pfeil: Ventil an der Mündung der Spermathekengänge; (c) frisch vom Weibchen ausgeschiedene Spermatophore, Toluidinblau, Pfeil: herausquellende Spermatozoen; (d) vom Schlaffaden abpräparierte Spermatophorenhülle, Direkttiefschwarz; (e) Semidünnschnitt, Hämatoxilin-Fuchsin; die Spermakammer enthält fadenförmige Spermatozoen und tröpfchenförmige akzessorische Sekrete.

H: Halsstück, Oc: Oviductus communis, S: Spermakammer, sM: schwammiges Material, Spg: Spermathekengang, sR: sklerotisierter Ring, vR: ventrales Receptaculum.
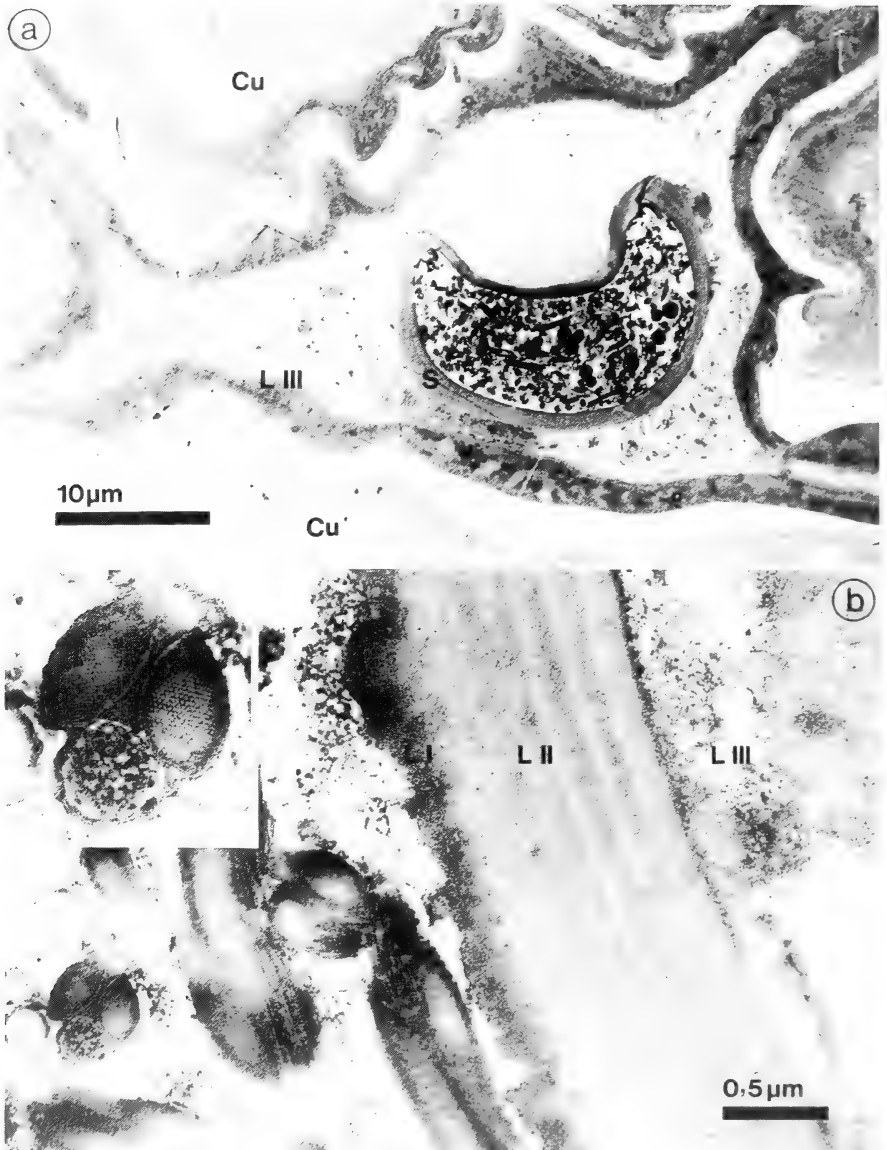
Abb.39: Spermatophore von *C. whitei*, Ultradünnschnitt durch den verjüngten Teil der Spermakammer, TEM. (a) Übersichtsaufnahme; (b) stärkere Vergrößerung, im linken Bildteil ist die Spermakammer mit mehreren Spermatozoen angeschnitten; Einsatz: Querschnitt durch den Hauptteil eines Spermatozoons (s. „Spermatozoen").

Cu: Cuticula der Vagina, L I—III: verschiedene Schichten der Spermatophorenwand, S: Spermakammer.

Der Spermatophorenhals kann nicht direkt in der richtigen Position gebildet werden. Der Fortsatz des Aedeagus kann wegen seines zu großen Durchmessers und seines Endhakens nicht so tief in die Spermathekengänge eingeführt werden, daß das Phallotrema direkt an deren Mündung zu liegen käme. Bei *Culicoides melleus* (Linley 1981a) wächst, aufgrund eines Druckanstiegs in der Spermatophore, der Hals nachträglich an einer vorgegebenen Stelle der Spermatophorenwand aus. Indem er in die Mündung der Spermathekengänge eindringt, wird durch deren Lumen seine äußere Form bestimmt. Es wäre denkbar, daß bei *C. whitei* ein ähnlicher Mechanismus existiert. Dies würde erfordern, daß das Material für den Spermatophorenhals zuletzt aus dem Phallotrema austritt. Beim anschließenden Auswachsen des Halses könnte dieser dem vom Fortsatz des Aedeagus geformten Kanal zur Mündung der Spermathekengänge folgen. Sollte das Weibchen durch aktives Verschließen seiner Spermathekengänge das Eindringen des Spermatophorenhalses verhindern, könnte es zu den oben geschilderten Mißbildungen mit umgebogenen Hälsen kommen.

Schicksal der Spermatophore

Nachdem der Spermatophorenhals mit den Spermathekengängen Kontakt aufgenommen hat, beginnen Spermatozoen und granuläres Material aus der Spermatophore in die Gänge zu strömen. In Nativpräparaten läßt sich beobachten, wie sich Material im verjüngten Teil der Spermakammer auflockert und in Richtung Halsstück bewegt. Im Spermatophorenhals und in beiden Spermathekengängen sieht man Spermatozoen in wellenförmiger Bewegung. Es konnte jedoch in keinem Fall eine aktive Fortbewegung der Spermatozoen erkannt werden. Auch ein Teil des granulären, stark anfärbbaren Materials gelangt aus der Spermatophore in beide Spermathekengänge (Abb.38a).

Nach der Kopulation werden in allen drei Spermatheken Spermatozoen gefunden. Das weitere Schicksal des granulären Sekrets konnte nicht verfolgt werden.

Innerhalb einer Stunde nach der Kopulation wird die mehr oder weniger entleerte Spermatophorenhülle vom Weibchen ausgeschieden (Abb.40). Während unmittelbar nach einer Kopulation in 93% der Fälle eine Spermatophore in der Vagina gefunden wurde, sank dieser Anteil schon nach 10 min auf 50%, nach 50 min auf 0%. Noch schneller nahm die Zahl derjenigen Spermatophoren ab, die in der ursprünglichen, dorsoventralen Lage im cranialen Teil der Vagina gefunden wurden. Innerhalb der ersten 2 Minuten nach der Kopulation nahmen über 90% der Spermatophoren diese Lage ein. Doch schon nach 2 Minuten waren 50% der gefundenen Spermatophoren deplaziert. Sie waren mit dem dicken Ende voran in Richtung Vulva gewandert. Die Spermakammern der deplazierten Spermatophoren erschienen oft eingedellt. Nach 30 min befand sich keine Spermatophore mehr in der ursprünglichen Position.

Wenn begattete Weibchen direkt nach der Kopulation unter einem Plastikdeckelchen auf einem Objektträger eingesperrt werden, können die ausgeschiedenen Spermatophoren später (mit etwas Glück) auf dem Objektträger gefunden werden (Abb.38c). Ausgeschiedene Spermatophoren weisen die ursprüngliche Form und Größe auf. Sie können noch etliche Spermatozoen enthalten, die dann aus der Öffnung des Spermatophorenhalses hervorquellen. Auch die Schlaffäden in den Käfigen sind mit ausgeschiedenen Spermatophorenhüllen übersät, die, in etwas Wasser abpräpariert, gut die ursprüngliche Form erkennen lassen (Abb.38d).
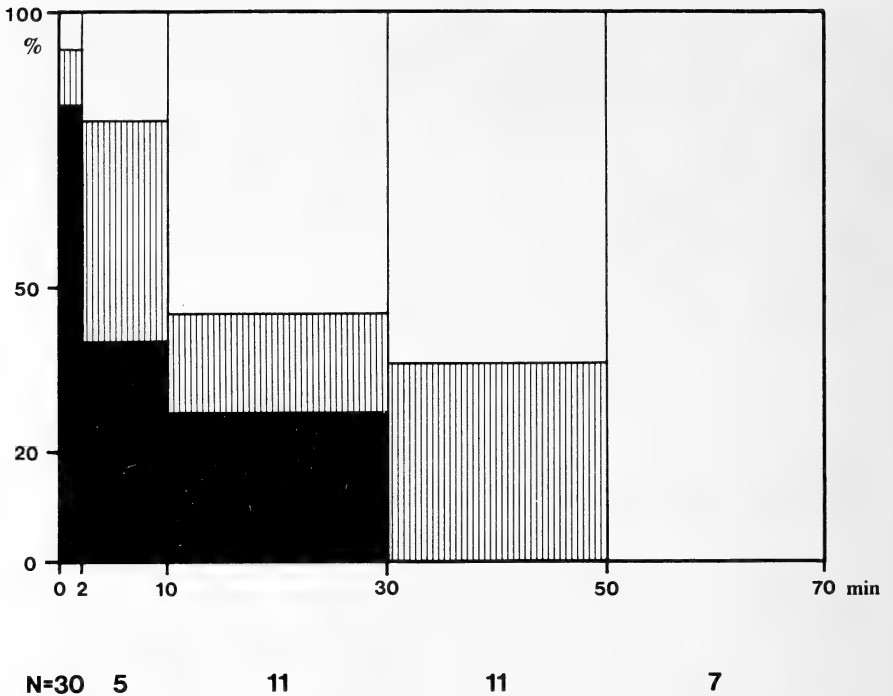
Abb.40: Spermatophoren in *C. whitei*-Weibchen in verschiedenen Zeitabständen nach der Kopulation. Abszisse: Zeit zwischen Kopulation und Fixierung in Minuten, unter den Zeitintervallen ist die Anzahl n der jeweils untersuchten Fälle angegeben; Ordinate: Ergebnis in % der untersuchten Fälle n. Schwarze Balken: Spermatophore in ursprünglicher Position; gestreifte Balken: Spermatophore deplaziert; weiße Balken: keine Spermatophore.

Anders als bei *Simulium decorum*, wo ein selektiver Transfer der Spermatozoen aus der Spermatophore in die einzelne Spermathek beobachtet wurde (Linley & Simmons 1983), werden bei *C. whitei* die Spermatozoen in alle drei Spermatheken transferiert. Der Befund, daß aus Spermatophoren mit umgebogenen Hälsen Spermatozoen und Granula in die Vagina geströmt waren, spricht dafür, daß ein Druckanstieg in der Spermakammer an dem Spermatransfer in die Spermatheken beteiligt ist. Der Mechanismus bedarf aber noch der Klärung (Diskussion 1.3).

Die Hüllen der Spermatophoren werden einige Zeit nach der Kopulation augeschieden, wie es auch bei den bisher bekannten spermatophorenbildenden Dipteren der Fall ist. Daß sie später nicht gefressen werden, beweisen die massenhaft an den Schlaffäden gefundenen Spermatophorenhüllen. Das Material der Spermatophorenwand kann also nicht als Beitrag zur Ernährung der Weibchen angesehen werden, wie beispielsweise bei den Orthoptera, bei denen das Weibchen den Rest der Spermatophore in der Regel auffrißt (Davey 1965, Mann 1984).

Die Entfernung der Spermatophore aus der Vagina ist möglicherweise eine notwendige Voraussetzung für den zur Befruchtung des nächsten Eies notwendigen Spermatozoentransfer aus den Spermathekengängen in das ventrale Receptaculum. Zum anderen könnte auf diese Weise die Rezeptivität des Weibchens wiederhergestellt werden. Nicht zuletzt bestimmt der Zeitpunkt des Ausschei-

dens der Spermatophore wahrscheinlich den Grad der Spermathekenfüllung durch den betreffenden Partner: sobald der Spermatophorenhals den Kontakt zur Genitalpapille verliert, ist der Spermatransfer in die Spermatheken beendet. Es ist nicht auszuschließen, daß danach weiterhin aus dem Spermatophorenhals ausströmende Spermatozoen in das ventrale Receptaculum gelangen und mit dort vorhandenen Spermatozoen in Konkurrenz treten (Diskussion 1.4.). Letzteres wäre jedoch nur durch eine aktive und gerichtete Fortbewegung der Spermatozoen möglich.

Sowohl Männchen als auch Weibchen kopulieren oft mehrfach hintereinander mit wechselnden Partnern (s. „Kopulation"). Die Männchen können dabei direkt hintereinander innerhalb von 45 min mindestens 5 Spermatophoren bilden (n = 2), eine größere Anzahl von aufeinanderfolgenden Kopulationen konnte in diesem Rahmen nicht untersucht werden. In mehrfach begatteten Weibchen (n = 10) wurde bisher immer nur eine einzige Spermatophore gefunden, selbst bei 2 Weibchen, die innerhalb von 100 Minuten 7 mal in unterschiedlichen Zeitabständen mit verschiedenen Männchen kopuliert hatten.

Wahrscheinlich kopuliert ein Weibchen nur dann erneut, wenn seine Vagina leer ist, wenn also entweder in der vorangegangenen Kopulation keine Spermatophore übertragen wurde ($\leq 7\%$ der untersuchten Fälle), oder diese bereits wieder ausgeschieden ist. Die Halbwertszeit für das Ausscheiden der Spermatophore liegt zwischen 10 und 30 min. Für das Ausräumen einer noch in der Vagina vorhandenen Spermatophore durch den nachfolgenden Kopulationspartner wurden keine Hinweise gefunden.

Eiablage

In seinem bis zu einem Jahr dauernden Leben kann ein *C. whitei*-Weibchen über 2000 Eier legen (Burkhardt & de la Motte 1987). In Laborversuchen betrug die tägliche Eiablagerate im Mittel 10 (± 6; n = 147) und maximal 26. Die individuellen Schwankungen von Tag zu Tag waren groß, ließen aber innerhalb eines Beobachtungszeitraumes von 14 Tagen keine Periodizität erkennen. Gesundheits- und Ernährungszustand der Weibchen haben erheblichen Enfluß auf die Eiablagerate. Hingegen bildet das Vorhandensein eines Spermavorrates keine notwendige Voraussetzung für die Eiablage, da auch jungfräuliche Weibchen Eier legen.

Die Eiablage erfolgt während des ganzen Tages, in den Morgen- und Abendstunden jedoch seltener (Abb.41). Es ist keine zeitliche Koppelung mit der Kopulationsaktivität feststellbar. Die Eier werden in der Regel einzeln mit der konvexeren Seite nach unten an das Substrat geklebt, so daß der Grat mit dem Plastron nach oben weist (Abb.6a). Es kommt auch vor, daß mehrere Eier dicht nebeneinander abgelegt werden, besonders dann, wenn Substratmangel herrscht. Die größte im Labor registrierte Eiablageleistung betrug 12 Eier innerhalb von 60 min, die kürzeste beobachtete Zeitspanne zwischen zwei aufeinanderfolgenden Eiablagen 45 s.

Eiablagesubstrat
Die Larvalentwicklung von *C. whitei* findet in verrottendem Pflanzenmaterial statt. Dementsprechend werden die Eier bevorzugt auf abgefallenen Pflanzenteilen abgelegt
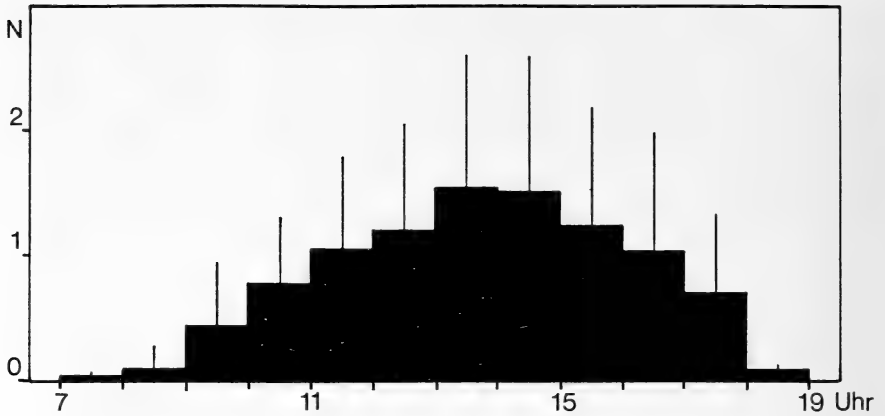
Abb.41: Eiablagehäufigkeit bei *C. whitei* im Tagesgang.

Abszisse: Zeit in 1-Stunden-Intervallen von Tagesanfang bis Tagesende; Ordinate: Die Balkenlänge zeigt die Zahl der abgelegten Eier pro Weibchen und Stunde, die senkrechten Striche geben die Standardabweichung an.

(Feijen 1989). Im natürlichen Habitat von *C. whitei* (Malaysia) wurden Diopsideneier an der Unterseite von zwei behaarten Hülsenfrüchten gefunden. Diese Eier stammten vermutlich von *C. whitei*-Weibchen, die sich unmittelbar vorher an diesen Früchten aufgehalten hatten. In der Zucht legen die Tiere ihre Eier auf verrottenden Maisblättern ab. In den Käfig gelegte Erbsenhülsen (*Pisum sativum*) werden ebenfalls gerne als Eiablagesubstrat angenommen.

Verhalten bei der Eiablage

Vor der Eiablage zeigen die Weibchen ein charakteristisches Verhalten. Langsam vorwärtslaufend berühren sie das Substrat häufig mit dem Rüssel. Gleichzeitig führen sie ihre ausgestreckten Cerci schleifend oder schnell tippend über den Untergrund. An manchen Stellen bleiben die Weibchen stehen und prüfen den Untergrund genauer, indem sie die Cerci vor- und zurückbewegen, oder sie in eine Ritze hineinstecken.

Ist eine geeignete Stelle gefunden, nimmt das Tier eine starre Haltung ein, wobei das Abdomenende maximal gestreckt ist. Manchmal wird ein weißes Spitzchen in der Vulva sichtbar. Die starre Haltung wird 8—15 s lang beibehalten (11±2 s; n=24). Dann wird ein Ei nach hinten aus der Vulva geschoben, während das Abdomen nach vorne über das Substrat weggezogen wird. Oft werden dabei tupfende Bewegungen ausgeführt, die zum Festkleben des Eies dienen könnten. Diese eigentliche Eiablage beansprucht nur ungefähr 1 s.

Wird das Weibchen wenige Sekunden nachdem es die starre Haltung eingenommen hat gestört, so wird der Eiablagevorgang abgebrochen und der Hinterleib erhält seine ursprüngliche Form zurück. Sind jedoch seit dem Einnehmen der starren Haltung mehr als 5 s verstrichen, so reagiert das Weibchen nur noch auf heftige Störungen, indem es

zur Seite weicht oder auffliegt. In jedem Fall wird der Eiablagevorgang dann jedoch vollendet, unabhängig davon, wo das Ei zu liegen kommt.

Während das Weibchen die starre Körperhaltung einnimmt, leitet es offensichtlich die Eiablage ein. Möglicherweise wird erst jetzt eine Ovulation ausgelöst, also ein Ei aus einer Ovariole in den Ovidukt entlassen, wie es bei *Musca domestica* (Degrugillier & Leopold 1973) und bei *Hippelates collusor* (Schwartz 1965) beschrieben ist.

Durch die maximale Streckung des Abdomenendes, und somit der Knickstelle im Oviductus communis, wird dem ablagereifen Ei der Weg in den caudalen Teil des Ovidukts freigegeben. Sobald das Ei, vorangetrieben durch die Peristaltik der Ovariolen und der Ovidukte, die Knickstelle passiert hat, kann die caudad verlagerte Vagina nicht mehr in ihre Ruheposition zurückkehren, die Eiablage muß beendet werden. Dieser Zeitpunkt dürfte nach ca. 5 s erreicht sein, da die Eiablage nach dieser Zeitspanne nicht mehr abgebrochen werden kann.

Bei *Musca domestica* beträgt die Verweildauer des Eies in der Vagina im Mittel 5,4 s (3,1—10,1) (Degrugillier & Leopold 1973). Dieser Wert ist gut mit der bei *C. whitei* gemessenen Eiablagedauer von 10,9 s (8—15) vergleichbar, wenn man die für die Oviduktpassage veranschlagten 5 s abzieht.

Vorgänge innerhalb der weiblichen Geschlechtsorgane während der Eiablage:

Werden Weibchen 5—8 s nach Einnehmen der starren Eiablagehaltung in flüssigem Stickstoff fixiert, so befindet sich fast immer ein Ei im Bereich der Vagina. Da diese
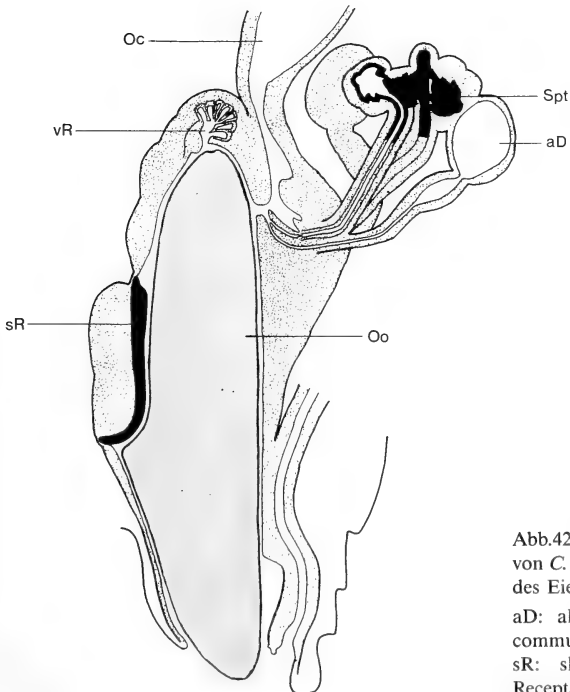
Abb.42: Innere weibliche Geschlechtsorgane von *C. whitei* zum Zeitpunkt der Besamung des Eies, Lateralansicht von links.

aD: akzessorische Drüse, Oc: Oviductus communis, Oo: Oocyte, Spt: Spermathek, sR: sklerotisierter Ring, vR: ventrales Receptaculum.

Abb.43: Weibliche Geschlechtsorgane von *C. whitei* während der Eiablage, Totalpräparate in Polyvinyl-lactophenol mit Direkttiefschwarz. (a) Übertritt des Eies aus dem Ovidukt in die Vagina, Lateralansicht von links; (b) während der Besamung, Ventralansicht.

C: Cercus, cEp: caudaler Eipol, D: Darm, Oc: Oviductus communis, Rm: am sklerotisierten Ring ansetzende Ringmuskulatur, Spt: Spermatheken, sR sklerotisierter Ring, VIII: Sternum 8, vR: ventrales Receptaculum, Vu: Vulva, Pfeil: Mikropyle, Balkenlänge jeweils 100 μm.

zu klein ist, um ein Ei in seiner ganzen Länge aufzunehmen, steckt das Ei entweder mit seinem cranialen Ende noch im Oviductus communis, oder sein caudales Ende steht schon aus der Vulva heraus (Abb.42, 43, 44).

Im leeren Zustand besitzt die Vagina von *C. whitei* äußere Abmessungen von ca. 650x250 μm und ein relativ enges Lumen (s. „Vagina"). Ein reifes Ei mißt ca. 840x240 μm (s. „Eier"). Aus diesem Größenvergleich läßt sich bereits ermessen, daß die Vagina beim Hindurchgleiten eines Eies star-

ken Verformungen ausgesetzt ist. Ihr Muskelschlauch wird gedehnt, die Cuticulafalten geglättet. Der anhand von Schnittpräparaten gemessene Cuticulaumfang von ca. 750 μm (Abb.12M) reicht dann aus, um ein Ei mit einem Umfang von ca. 730 μm (ebenfalls an Schnittpräparaten gemessen) passieren zu lassen.

Nur in einem Fall gelang es, ein Weibchen während des Übertritts des Eies aus dem Ovidukt in die Vagina zu fixieren (Abb.43a). Der Ovidukt und der craniale Bereich der Vagina ist in dieser Phase stark ausgeweitet, das ventrale Receptaculum aus seiner Ruheposition nach ventral verdrängt. Die Mündungen der Gänge von Spermatheken und akzessorischen Drüsen weisen nach caudal.

Die restlichen Präparate wurden stets in einem späteren Stadium fixiert: Der craniale Eipol mit der Mikropyle steckt in der Mündung des ventralen Receptaculum, das infolgedessen nach cranial verlagert ist (Abb.42, 44). Die ventrale Aussackung caudal vom ventralen Receptaculum ist gestreckt. Die konvexere Unterseite des Eies liegt dem ventralen sklerotisierten Ring an, und das caudale Ende ragt mehr oder weniger aus der Vulva heraus. Die Mündungen der Gänge von Spermatheken und akzessorischen Drüsen weisen nun nach cranial (Abb.10b, 44), die Spermathekengänge sind durch Cuticulawülste im Mündungsbereich dicht verschlossen. Die Kammern des ventralen Receptaculum enthalten in diesen Präparaten mehr Spermatozoen als in Präparaten von begatteten Weibchen, deren Fixierung nicht während einer Eiablage erfolgte (s. „ventrales Receptaculum").

Die Mikropyle des Eies bildet einen vorgefertigten Einlaß für Spermatozoen, welche hier zur Dottermembran vordringen können, um das Ei zu befruchten (Weber 1933, Retnakaran & Percy 1985). Indem die Mikropyle in die Öffnung des ventralen Receptaculum gepreßt wird, wird eine Besamung des Eies durch Spermatozoen aus den Kammern des ventralen Receptaculum ermöglicht. Gleichzeitig ist der Zugang für Spermatozoen aus den Spermathekengängen versperrt.

Daß die Besamung des Eies nicht an der Mündung der Spermathekengänge sondern an einem ventralen Receptaculum erfolgt, ist bei den höheren Dipteren kein Einzelfall. Die Literatur enthält vergleichbare Befunde beispielsweise für *Drosophila melanogaster* (Miller 1965), *Dacus oleae* (Solinas & Nuzzaci 1984) und *Musca domestica* (Leopold 1973). Es gibt jedoch auch Fälle, bei denen die Besamung des Eies direkt an den Spermathekengängen erfolgen soll, zum Beispiel bei *Glossina morsitans* (Roberts 1973). In allen zitierten Arbeiten wurde nachgewiesen, daß die Mikropyle des Eies bei der Eiablage vorübergehend in engen Kontakt mit der Mündung des entsprechenden Spermatozoenspeichers tritt.

Um im Zuge der Eiablage möglicherweise auftretende Veränderungen im Bereich der Mikropyle zu erfassen, wurden aus dem Ovar herauspräparierte Eier und abgelegte Eier im REM untersucht. Auf der Mikropyle von dem Ovar entnommenen Eiern wurde eine kappenartige Sekretauflagerung gefunden, die bei abgelegten Eiern fehlt (Abb.6c,d). In den Schnittpräparaten von Eiern im Stadium der Besamung am ventralen Receptaculum konnte ebenfalls keine Sekretkappe nachgewiesen werden (Abb.15).

Leopold et al. (1978, 1980) beschrieben eine ähnliche, die Mikropyle bedeckende Sekretkappe bei Eiern aus dem Ovidukt von *Musca domestica*. Diese „cap substance" soll möglicherweise ein Rezeptorsystem für die Spermatozoen enthalten und an der Auslösung der Akrosomenreaktion beteiligt sein. Leopolds Untersuchungen zeigten weiter, daß die Sekretkappe im Zuge des Befruchtungsvorganges aufgelöst wird. An der Auflösung sind sowohl lytische Sekrete aus den akzessori-
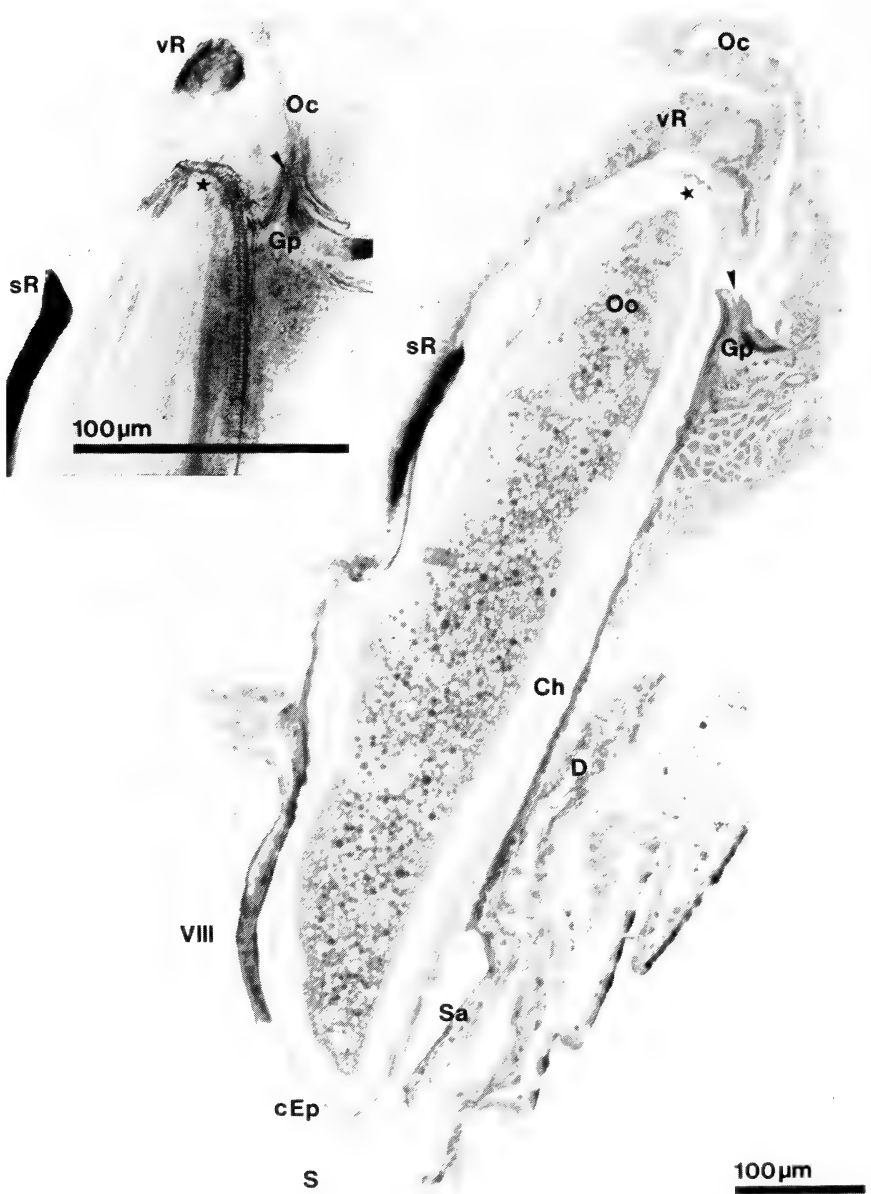
Abb.44: Weibliche Geschlechtsorgane von *C. whitei* während der Besamung des Eies, medianer Semi-dünnschnitt, Richardson (Ausschnittsvergrößerung hieraus in Abb.15); Einsatz: Totalpräparat in Polyvi-nyllactophenol mit Direkttiefschwarz, Lateralansicht von links.

cEp: caudaler Eipol, Ch: Chorion, D: Darm, Gp: Genitalpapille, Oc: Oviductus communis, Oo: Ooplasma, S: Seta auf Subanalplatte, Sa: Subanalplatte, sR: sklerotisierter Ring, vR: ventrales Recepta-

schen Drüsen des Weibchens beteiligt, als auch die mechanische Einwirkung von Cuticuladornen in der ventralen Befruchtungskammer.

Ein ähnlicher Vorgang ist bei *C. whitei* denkbar. Entsprechende Cuticulaborsten finden sich sowohl in der Mündung des ventralen Receptaculum (Abb.11d, 14), als auch zwischen den Cuticulakammern desselben Organs (s. „ventrales Receptaculum"). Das Borstenfeld in der Mündung scheint darüberhinaus von seiner Lage und Struktur her geeignet, schon vor der Eiablage an der gegenüberliegenden Mündung der akzessorischen Drüsen mit Sekret beladen zu werden, welches dann gezielt auf die Sekretkappe aufgebracht werden könnte.

Bei einigen abgelegten Eiern waren in der Nähe der Mikropyle 4—6 fadenförmige Strukturen aufgelagert, bei denen es sich der Größe und der Gestalt nach um Spermatozoen handeln dürfte (Abb.6d). Für diese Deutung spricht auch ihre Lagerung in Schleifen von rund 8 μm Durchmesser (s. „Spermatozoen").

Das Vorkommen von Polyspermie bei Dipteren wird von verschiedenen Autoren kontrovers diskutiert (Lefevre & Jonsson 1962, Hildreth & Lucchesi 1963, Sonnenblick 1965, Sivinsky 1979, Letsinger & Gromko 1985, Smith et al. 1988). Die Mehrzahl der Autoren kommt zu dem Ergebnis, daß mehrere Spermatozoen in die Mikropyle des Eies eindringen, wenn auch nur eines davon tatsächlich die Befruchtung vollzieht (Retnakaran & Percy 1985). Degrugillier & Leopold (1973) geben für *Musca domestica* einen Polyspermiegrad von 1—4 Spermatozoen pro Ei an. Mit diesem Befund stehen die Beobachtungen bei *C. whitei* im Einklang.

Aus den bisherigen Befunden läßt sich folgender Ablauf der Eiablage als plausibel annehmen:

Solange die Vagina leer ist, liegt die Mündung der Spermathekengänge in unmittelbarer Nähe zum ventralen Receptaculum, Spermatozoen können passieren. Da bei Weibchen, die während der Eiablage fixiert wurden, mehr Spermatozoen im ventralen Receptaculum gefunden wurden als bei anderen Weibchen, scheint vor der Eiablage ein Spermatozoentransfer aus den Spermatheken ins ventrale Receptaculum stattzufinden, wie es für *Hippelates collusor* (Schwartz 1965), *Musca domestica* (Degrugillier & Leopold 1973) und *Dacus oleae* (Solinas & Nuzzaci 1984) beschrieben ist. Dabei wird wahrscheinlich die Öffnung des ventralen Receptaculum dicht an die dorsal gegenüberliegende Genitalpapille gepreßt. Für den Spermatozoentransport kommen, abgesehen von der bisher nicht einschätzbaren Fähigkeit der Spermatozoen zu aktiver Fortbewegung, mehrere Mechanismen in Frage. Brüel (1897) vermutete, daß die Spermatozoen durch das Sekret der Spermatheken hinausgeschwemmt werden. Da hier nur kleine Volumina zu transportieren sind, wäre auch eine Beteiligung der wippenden Bewegung der Spermathekengänge denkbar. Solinas & Nuzzaci (1984) nehmen an, daß bei *Dacus oleae*, die ein sehr ähnlich gebautes ventrales Receptaculum („fertilization chamber") besitzt, die dort inserierenden „extrinsischen Muskeln" einen Unterdruck bewirken, der Spermatozoen aus der Mündung der Spermathekengänge ansaugt. Eine ähnliche Wirkung wäre bei *C. whitei* auch denkbar, obwohl die angesprochenen Muskeln nicht direkt vergleichbar sind (s. „ventrales Receptaculum"). Gleichzeitig wird möglicherweise Sekret

culum, VIII: Sternum 8, Pfeil: Mündung der Spermathekengänge, Stern: Mikropylpol. Der Hohlraum zwischen Chorion und Ooplasma ist ein Schrumpfungsartefakt.

aus den akzessorischen Drüsen auf das Borstenfeld in der Mündung des ventralen Receptaculum aufgebracht.

Wurde ein geeignetes Substrat zur Eiablage ertastet, so wird dem Ei durch Strecken der Genitalien die Passage des Oviduktes ermöglicht. Danach kann die Eiablage nicht mehr abgebrochen werden. Beim Übergang des Eies aus dem Ovidukt in die Vagina wird das ventrale Receptaculum nach ventral verdrängt und dabei möglicherweise auch komprimiert. Eine Spermatozoenpassage aus den Spermatheken ins ventrale Receptaculum ist nun nicht mehr möglich. In der Vagina verbliebene Spermatozoen oder Spermatophorenreste werden vom caudalen Ende des Eies aus der Vulva geschoben.

Nachdem das Ei den Ovidukt verlassen hat, wird das ventrale Receptaculum durch die daran ansetzenden Muskelbänder (Lm III, Kap. „Vagina") in seine ursprüngliche Position zurückgezogen, wobei sein Eingang über der Mikropyle zu liegen kommt. Das caudale Ende des Eies ragt bereits aus der Vulva heraus. Von diesem Zeitpunkt an steht das schon vorher gasgefüllte Plastron mit der Atmosphäre in Gasaustausch. Die plötzlich veränderte Zusammensetzung dieser Gashülle, beispielsweise ein höherer Sauerstoffgehalt, könnte bei der anschließenden Befruchtung eine Rolle spielen.

Das Ei wird nun in der Vagina craniad bewegt. Die Verlagerung des ventralen Receptaculum nach cranial und die damit verbundene Streckung des ventralen cranialen Vaginabereiches bezeugen, daß der craniale Eipol mit einiger Kraft in die Mündung des ventralen Receptaculum gestoßen wird. In dieser Position wird die Sekretkappe auf der Mikropyle aufgelöst. Spermatozoen dringen aus den Kammern des ventralen Receptaculum zur Mikropyle vor und befruchten das Ei (Diskussion 1.2). Der Zugang von den Spermathekengängen her ist durch die Verformung der Vagina abgedichtet.

Durch das Zusammenspiel der kräftigen Ring- und Längsmuskulatur der Vagina wird das Ei aus der Vulva hinausgeschoben.

DISKUSSION

Die Diskussion der einzelnen Befunde zur Morphologie und Funktion des Reproduktionssystems von *Cyrtodiopsis whitei* ist in den Ergebnisteil integriert. Die abschließende Diskussion kehrt nun zu jenen Fragen zurück, die Anlaß zu unseren Untersuchungen gegeben hatten. Ihr erster Teil befaßt sich mit funktionellen Aspekten des Reproduktionssystems von *C. whitei*. Die hohe Kopulationshäufigkeit und Promiskuität von *C. whitei* wird mit den neu erworbenen Kenntnissen über die zur Verfügung stehenden Spermatozoenspeicherorgane des Weibchens und die Vorgänge bei Kopulation und Eiablage in Beziehung gesetzt. Dabei kann die Zahl der übertragenen, gespeicherten und zur Befruchtung der Eier verwendeten Spermatozoen vorerst nur geschätzt werden, da Spermatozoenzählungen sowie Versuche mit markierten Spermatozoen bisher nicht durchgeführt wurden. Des weiteren werden die Funktion des gekammerten ventralen Receptaculum und der Spermatophore von *C. whitei*, sowie die Möglichkeiten einer Spermakonkurrenz diskutiert. Im zweiten Teil der Diskussion werden einige herausra-

gende Merkmale des Reproduktionssystems von *C. whitei* mit entsprechenden Literaturbefunden aus anderen Dipterenfamilien in Verbindung gebracht und so auf ihre Eignung für eine vergleichende Untersuchung zur Klärung von Verwandtschaftsbeziehungen geprüft.

1. Funktionelle Aspekte des Reproduktionssystems von *C. whitei*

1.1 Abschätzung der übertragenen, gespeicherten und zur Befruchtung der Eier verwendeten Spermatozoenzahl

Während der Kopulation produziert das Männchen in der Vagina des Weibchens eine Spermatophore, deren einzige Spermakammer ein Volumen[2]) von ca. 60 x 10^3 μm³ hat. Bei einem Spermatozoenvolumen[3]) von näherungsweise 23 μm³ würde sie also rein rechnerisch ca. 2500 Spermatozoen Platz bieten. Tatsächlich enthält eine Spermatophore von *C. whitei* jedoch wesentlich weniger Spermatozoen, da diese in einem Gemisch aus Drüsensekreten locker verteilt liegen (s. „Spermatransfer mittels Spermatophore"). Die Spermatozoenzahl dürfte sich damit auf weniger als die Hälfte reduzieren, so daß bei einer Kopulation wahrscheinlich nicht mehr als 1000 Spermatozoen übertragen werden. Da aus einer Kopulation mehr als 200 Nachkommen hervorgehen können (Burkhardt et al. 1991), muß die übertragene Spermatophore mindestens ebensoviele Spermatozoen enthalten, je nach angenommenem Polyspermiegrad ein entsprechend Vielfaches. Ein Spermatozoengehalt zwischen 200 und 1000 Spermatozoen erscheint auch nach dem histologischen Bild der Spermatophore realistisch.

Die Spermatozoen aus einer Spermatophore gelangen in alle drei Spermatheken, es findet keine selektive Speicherung statt. Die drei Spermatheken haben ein gemeinsames Volumen[4]) von ca. 150 x 10^3 μm³, was etwa dem Volumen von drei Spermatophoren entspricht. Da die Spermatozoen in den Spermatheken jedoch viel dichter liegen als in den Spermatophoren, sind mehr als drei Spermatophoren nötig um die Spermatheken vollständig zu füllen. Das Volumen der Spermatheken entspricht dem von ca. 6400 Spermatozoen.

In Laborversuchen kopulierten Weibchen von *C. whitei* im Mittel 17 mal pro Tag, die höchste im Labor registrierte Anzahl an Kopulationen pro Tag betrug 34. Selbst wenn man von einem Mittelwert von nur 200 Spermatozoen pro Spermatophore ausgeht,

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[2]) Das Spermatophorenvolumen wurde näherungsweise als Kugelvolumen berechnet ($V = 4/3\, r^3 \pi$): Bei einem Durchmesser von ca. 48 μm ergibt sich ein Volumen von ca. 57 x 10^3 μm³.

[3]) Das Spermatozoenvolumen wurde näherungsweise als Zylindervolumen berechnet ($V = r^2 \pi\, L$): Bei einem Durchmesser von ca. 0,4 μm und einer Länge von 178 μm ergibt sich ein Volumen von ca. 23 μm³. Bei kompakter Füllung hätten also mehr als 2531 Spermatozoen in einer Spermatophore Platz.

[4]) Das Spermathekenvolumen wurde näherungsweise als Kugelvolumen berechnet ($V = 4/3\, r^3 \pi$): Bei einem Innendurchmesser von ca. 45 μm ergibt sich ein Volumen von ca. 48 x 10^3 μm³. Das Volumen von 3 Spermatheken entspräche bei kompakter Füllung also ca. 6411 Spermatozoen.

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wäre es also denkbar, daß die Spermatozoenspeicherkapazität eines Weibchens durch die Kopulationen eines einzigen Tages erreicht wird. Inwieweit die im Labor beobachtete Kopulationsaktivität mit den Verhältnissen im natürlichen Habitat vergleichbar ist, kann nicht beurteilt werden, da kaum Vergleichsdaten verfügbar sind. Es liegt jedoch eine Freilandbeobachtung vor, bei der ein Weibchen 26 mal hintereinander kopulierte.

Da die Weibchen nicht nur an einem Tag mehrfach kopulieren, sondern dies auch täglich wiederholen, muß entweder die gespeicherte Spermatozoenmenge zwischenzeitlich stark reduziert werden, oder es können keine neuen Spermatozoen in die Spermatheken aufgenommen werden. Eine Reduktion der gespeicherten Spermatozoenmenge wäre durch einen hohen Polyspermiegrad bei der Besamung der Eier denkbar, durch aktives Ausscheiden oder durch Auflösen der Spermatozoen. Derartiges Vorgehen scheint unvorteilhaft, solange zukünftige Kopulationschancen für das Weibchen nicht einschätzbar sind, sollte also nur unmittelbar vor einer neuen Kopulation oder in deren Anfangsphase in Frage kommen. Andererseits scheint es auf die Dauer nachteilig, zugunsten von bereits lange Zeit gespeicherten Spermatozoen auf frische Spermatozoen zu verzichten.

In Laborversuchen legten Weibchen im Mittel 10 Eier pro Tag. Das Verhältnis von Kopulationen pro Tag zu Eiablagen pro Tag war also größer als 1. Prinzipiell könnte demzufolge jedes Ei durch eine gesonderte Kopulation befruchtet werden. Diese Möglichkeit ist jedoch auszuschließen, da Kopulationen und Eiablagen nicht abwechselnd aufeinander folgen, sondern je nach Gelegenheit und zeitlich voneinander unabhängig geschehen.

Eine einzige Kopulation kann zur Befruchtung von über 200 Eiern ausreichen (Burkhardt et al. 1991). Möglicherweise wären also schon 10 Kopulationen ausreichend, um die ca. 2000 Eier zu befruchten, die ein Weibchen im Laufe seines Lebens legt (Burkhardt & de la Motte 1987). Anders betrachtet, könnte rein hypothetisch eine einmalige vollständige Füllung der Spermatheken ($\leq$6400 Spermatozoen) ausreichen, um diese Eier zu befruchten. Geht man aber von einem Polyspermiegrad von mehr als 3 Spermatozoen pro Ei aus, so werden weitere Kopulationen notwendig. Das gleiche gilt für den Fall, daß die Spermatozoen nach einiger Zeit absterben. Die längste bisher registrierte Zeitspanne nach einer Kopulation, nach der noch befruchtete Eier gelegt wurden, betrug 7 Wochen (eigene Untersuchungen).

1.2 Funktion des ventralen Receptaculum

Das ventrale Receptaculum von *C. whitei* ist distal in 30—40 Kammern unterteilt, die um das Ende eines kurzen Ganges gruppiert sind. An der Mündung dieses Ganges in die Vagina findet die Besamung der Eier statt (s. „Eiablage"). Zu diesem Zweck werden vor der Eiablage Spermatozoen aus den Spermatheken ins ventrale Receptaculum transferiert, wo sie dann eng aufgerollt im distalen Teil der Cuticulakammern liegen. Während die Spermatheken von *C. whitei* als Langzeitspeicher für große Spermatozoenmengen verstanden werden können, dient das ventrale Receptaculum also eher als Zwischenlager für eine geringere Anzahl von Spermatozoen. Obwohl dem ventralen Receptaculum von *C. whitei* in Struktur und Funktion ähnliche Organe bereits bei Tephritidae

bereits bei Tephritidae und Otitidae beschrieben wurden (Diskussion 2.2), liegt bisher keine funktionelle Erklärung für die distale Kammerung vor.

Durch die gefächerte Anordnung der Kammern haben in verschiedenen Kammern liegende Spermatozoen eine in Bezug auf die Mikropyle des zu befruchtenden Eies relativ gleichwertige Ausgangsposition. Es ist die Möglichkeit einer Spermatozoenkonkurrenz im engsten Sinne gegeben, bei der das Spermatozoon die Eizelle befruchtet, welches die Mikropyle am ehesten erreicht.

Die Spermatozoen von *C. whitei* können schlagartig aus der aufgerollten Form (Durchmesser $\geqq 6,6$ μm) in eine gestreckte übergehen (Länge ca. 178 μm, jedoch mehr oder weniger stark geschlängelt, Kap. „Spermatozoen"). Es wäre vorstellbar, daß durch diesen „Sprungfedermechanismus" die maximal 60 μm vom distalen Ende einer Cuticulakammer bis zur Mikropyle am Eingang des Receptaculum in kürzester Zeit überwunden werden. Zur Besamung der Eier steht ja vermutlich nur ein Zeitraum von etwa 3—10 s zur Verfügung (s. „Eiablage"). Der Durchmesser der Cuticulakammern (6,7—7,5 μm bei C. whitei; ca. 6 μm bei *Dacus oleae* (Tephritidae, Solinas & Nuzzaci 1984)) stimmt mit dem Durchmesser eng aufgerollter Spermatozoen überein. Die Kammerung des ventralen Receptaculum könnte also gut als Anpassung an derartige Vorgänge verstanden werden. Daß Solinas & Nuzzaci (1984) bei der Untersuchung des ventralen Receptaculum von *Dacus oleae* einen ähnlichen Eindruck gewannen, legt die diesbezügliche Formulierung „...spermatozoon lodged in it as ready to spring" nahe.

1.3 Funktion der Spermatophore

Im Gegensatz zu den meisten Dipteren erfolgt bei *C. whitei* die Spermaübertragung mit Hilfe einer Spermatophore. Einige der für das Vorkommen von Spermatophoren in Frage kommenden Erklärungen können hier von vornherein ausgeschlossen werden. So trägt bei *C. whitei* die Spermatophore selbst sicher nicht zur Ernährung des Weibchens (Davey 1965, Thornhill 1976b, Mann 1984) bei, sie wird vom Weibchen nach einiger Zeit unverdaut ausgeschieden. Auch kann eine im Weibchen abgesetzte Spermatophore höchstens für kurze Zeit im Sinne eines „mating plug" weitere Kopulationen verhindern, da das Ausscheiden der Spermatophore oft schon nach wenigen Minuten erfolgt. Da auch jungfräuliche Weibchen Eier legen, und da bereits begattete Weibchen auch weiterhin kopulieren, werden diese Verhaltensweisen höchstens in geringem Maße durch eine mit der Spermatophore verbundene chemische oder mechanische Stimulation graduell beeinflußt. Wahrscheinlich besteht die Funktion der Spermatophore von *C. whitei* also hauptsächlich in der Übertragung von Sperma.

Die Spermatophore bildet zusammen mit den Spermathekengängen und Spermatheken ein geschlossenes System. Sie verhindert, daß das Ejakulat von der günstigen Ausgangsposition an der Mündung der Spermathekengänge wegfließt oder verdrängt wird (Khalifa 1949, Davey 1965). *C. whitei*-Weibchen kopulieren oft in schneller Folge mit verschiedenen Partnern. Bei freier Spermaübertragung würden die Ejakulate der verschiedenen Männchen in der Vagina vermengt und als Gemisch in die Spermathekengänge gelangen, während bei Verwendung einer Spermatophore immer nur das Ejakulat eines Männchens zur Zeit Zugang zu den Spermathekengängen hat. Hieraus resultieren ganz

tieren ganz andere Möglichkeiten zu weiblicher Zuchtwahl, Konkurrenz der Männchen und ihrer Spermatozoen (Diskussion 1.4).

Solange der Kontakt zwischen Spermatophorenhals und Spermathekengängen besteht, können die Spermatozoen aus der Spermakammer nur in die Spermatheken gelangen, anstatt sich im gesamten weiblichen Reproduktionstrakt zu verteilen. In welchem Maße sich die Spermatozoen innerhalb der weiblichen Geschlechtsorgane aktiv fortbewegen ist unbekannt (s. „Spermatozoen"). Auf jeden Fall muß ein zusätzlicher Transportmechanismus existieren, denn auch akzessorische Sekrete gelangen aus der Spermatophore in die Spermatheken. Da die Spermathekengänge von *C. whitei* nicht zu einer peristaltischen Bewegung fähig sind (s. „Spermatheken"), ist ein derartiger Transport nur über Druckunterschiede zwischen der Spermamasse auf der einen und dem Spermathekenlumen auf der anderen Seite vorstellbar. Dabei ist die Effektivität in einem geschlossenen System wesentlich besser als in einem teilweise (mating plug) oder ganz offenen System (Absetzen freien Spermas in der Vagina).

Tatsächlich gibt es Hinweise darauf, daß Druckunterschiede beim Spermatransfer aus der Spermatophore eine Rolle spielen (s. dort). Der Befund, daß aus den Spermatophoren mit umgebogenen Hälsen Spermatozoen und Granula in die Vagina geströmt waren, spricht für einen Druckanstieg in der Spermakammer. Hier ist ein aktives Auspressen der Spermatophore durch die weibliche Vaginamuskulatur in Erwägung zu ziehen. Die häufig eingedellte Form deplazierter Spermatophoren in den Weibchen könnte, wenn es sich nicht um ein Fixierungsartefakt handelt, auf eine mechanische Krafteinwirkung hinweisen. Schwellkörper, wie sie von den Spermatophoren der Grillen bekannt sind (Davey 1965), wurden in der Spermatophore von *C. whitei* nicht gefunden.

Bei *Culicoides melleus* wurde ein osmosegetriebener Flüssigkeitseinstrom in die Spermatophore nachgewiesen und eine gleichzeitige Flüssigkeitsresorption in den Spermatheken des Weibchens gefordert (Linley & Simmons 1981c). Giglioli (1963) schlägt in einer Arbeit über *Anopheles gambiae* ebenfalls ein partielles Vakuum in den Spermatheken während der Spermaübertragung vor. Auch bei *C. whitei* ist der Transfer von Spermatozoen und granulärem Material aus der Spermatophore in die englumigen Spermathekengänge ohne eine Flüssigkeitsresorption am anderen Ende der Gänge, also in den Spermatheken, schwer vorstellbar, da die Spermatheken ein festes Volumen haben. Bisher konnte eine derartige Resorption jedoch weder bei *C. whitei* noch bei einer anderen Diptere nachgewiesen werden. Ansatzpunkte zu einer weiteren Untersuchung dieses Problems bei *C. whitei* bietet möglicherweise die Differenzierung des Epithels im distalen Teil der Spermathekengänge zu einem Transportepithel, sowie die teilweise fast kristalline Ultrastruktur des Inhalts der Spermathekendrüsen (s. „Spermatheken").

Das Schicksal des stark anfärbbaren, granulären Materials aus den Spermatophoren muß noch geklärt werden. Akzessorische Sekrete stellen bei Insekten einen wichtigen Bestandteil des Ejakulats dar (Pollock 1972, Leopold 1976, Hinton 1974, Mann 1984), und bei einigen Dipteren existieren spezielle Anpassungen zu ihrer Übertragung (Pollock 1972, Lewis & Pollock 1975). Möglicherweise ist die Spermatophore von *C. whitei* auch als Anpassung in dieser Richtung zu verstehen.

Bei Verwendung einer Spermatophore bleibt das geschlossene System auch nach Beendigung der Kopulation erhalten. So kann bei *C. whitei*, wie auch bei *Glyptotendipes paripes* (Nielsen 1959) und *Simulium decorum* (Linley & Simmons 1983), noch nach dem Ende der Kopulation ein Spermatransfer aus der Spermatophore in die Spermatheken stattfinden (Tab.4). Dadurch wird es prinzipiell möglich, die Kopulationsdauer zu verkürzen. Die Kopulationsdauern sind bei *C. whitei* mit ca. 45 s und bei der nach eigenen Untersuchungen ebenfalls Spermatophoren verwendenden Schwesterart *C. dalmanni* mit 30 s (Tan 1965) kurz im Vergleich zu den Mitgliedern anderer Diopsidengattungen, die mehrere Minuten bis Stunden kopulieren (Descamps 1957, Feijen 1989, Wickler & Seibt 1972). Eine Untersuchung von Diopsidenarten mit längerer Kopulationsdauer auf das Vorkommen von Spermatophoren könnte Aufschluß darüber geben, ob diese Unterschiede mit der Verwendung einer Spermatophore zusammenhängen. Der Vergleich der Kopulationsdauern der spermatophorenbildenden Dipteren aus verschiedenen Familien (Tab.4) ergibt allerdings neben ebenfalls sehr kurzen Kopulationsdauern bei *Glyptotendipes paripes* (Nielsen 1959) und *Simulium decorum* (Linley & Simmons 1983) auch sehr lange bei *Plecia nearctica* (Leppla et al. 1975) und *Glossina austeni* (Pollock 1974).

1.4 Spermakonkurrenz

„The clear conclusion is a sad one from a male's perspective: copulation does not always result in insemination, and insemination does not always result in fertilization" (Eberhard 1985).

Bei der hohen Kopulationshäufigkeit und Promiskuität der Weibchen von *C. whitei* muß das Vorkommen von Spermakonkurrenz in Erwägung gezogen werden. Unter dem Begriff „Spermakonkurrenz" werden im allgemeinen all jene Phänomene diskutiert, die nach aufeinanderfolgenden Kopulationen zu einer Ungleichverteilung der Vaterschaft führen. Hierzu sind in jüngerer Zeit verschiedene Arbeiten erschienen, die hauptsächlich auf theoretischen Überlegungen oder auf Versuchen mit diversen Vaterschaftsnachweisen basieren (Lefevre & Jonsson 1962, Parker 1970, Childress & Hartl 1972, Linley 1975, Lloyd 1979, Thornhill & Alcock 1983, Newport & Gromko 1984, Smith 1984, Parker 1991). Für einen statistisch nachgewiesenen Fortpflanzungsvorteil des größten, des erst- oder letztkopulierenden Männchens wurde fast immer eine plausible theoretische Erklärung gefunden. Die morphologischen und physiologischen Ursachen (Mechanismus) blieben jedoch in der Regel ungeklärt.

Die in Frage kommenden Ursachen lassen sich den Kategorien „weibliche Zuchtwahl", „Konkurrenz der Männchen", „Spermakonkurrenz" und „Spermatozoenkonkurrenz" zuordnen (Davey 1985, Eberhard 1985), die im folgenden kurz definiert und in Bezug auf ihr Vorkommen bei *C. whitei* diskutiert werden:

a) Weibliche Zuchtwahl,

wenn das Weibchen das Sperma eines Männchens bevorzugt in die Speicherorgane aufnimmt oder zur Befruchtung der Eier verwendet, aktiv ausscheidet, auflöst oder ähnliches.

Voraussetzungen: Das Weibchen ist in der Lage die Spermaaufnahme und -abgabe aktiv zu beeinflussen, Sperma aus verschiedenen Kopulationen mehr oder weniger getrennt zu speichern und freizusetzen, bzw. Sperma aufzulösen.

Effekt: Der Vaterschaftsanteil hängt von den Qualitäten des Männchens ab und ist unabhängig von der Reihenfolge der Kopulationen.

Für weibliche Zuchtwahl noch während oder nach der Kopulation („cryptic female choice" (Thornhill 1976b)) bestehen bei *C. whitei* mindestens zwei Möglichkeiten: 1) Die Weibchen besitzen die erforderlichen cuticulären Strukturen und Muskeln, um die Mündung der Spermathekengänge zu verschließen, so daß der Spermatophorenhals nicht eindringen kann (s. „Spermatransfer mittels Spermatophore"). Auf diese Weise wird eine Aufnahme von Sperma in die Spermatheken unterbunden. 2) Indem die Weibchen die Spermatophoren aktiv ausscheiden, bestimmen sie über die Dauer des Spermatransfers und damit über die in die Spermatheken aufgenommene Spermamenge.

Es gibt keine Hinweise auf einen Mechanismus zur getrennten Speicherung von Sperma aus aufeinanderfolgenden Kopulationen. Wenn Spermatransfer in die Spermatheken stattfindet, dann gelangt das Sperma in alle drei Spermatheken.

Da die Weibchen sehr häufig kopulieren, ist anzunehmen, daß zwischenzeitlich die gespeicherte Spermamenge reduziert wird (Diskussion 1.1). Auch dazu gibt es aber noch keine Befunde.

b) Konkurrenz der Männchen,

wenn ein Männchen das Sperma des Vorgängers mit den Genitalien ausräumt oder deplaziert.

Voraussetzungen: Entsprechende Ausbildung der männlichen Genitalien und Zugänglichkeit der weiblichen Spermaspeicher.

Effekt: Der Vaterschaftsanteil des letzten Männchens ist höher als der des Vorgängers.

Da *C. whitei*-Weibchen oft in schneller Folge mehrmals hintereinander kopulieren, wäre es prinzipiell denkbar, daß ein Männchen das Sperma des Vorgängers deplaziert oder aus der Vagina ausräumt, wie es bei Odonaten beschrieben wurde (Waage 1979). Die hakenförmig nach innen gebogenen Epiphallusschaufeln scheinen dazu geeignet. Außer dem Befund, daß nie zwei Spermatophoren in einem Weibchen gefunden wurden, gibt es auf ein derartiges Ausräumen jedoch keinerlei Hinweise. Bereits in die Spermatheken aufgenommenes Sperma ist für die Genitalien eines nachfolgenden Männchens ebenso unerreichbar wie die Spermatozoen im ventralen Receptaculum.

c) Spermakonkurrenz,

wenn das Sperma eines Männchens durch das eines Nachfolgers aus den Speicherorganen des Weibchens verdrängt, oder innerhalb dieser Speicherorgane in eine ungünstigere Position verdrängt oder durch Sekrete des Nachfolgers abgekapselt wird. Als Spermakonkurrenz gilt außerdem, wenn das Sperma eines Männchens durch das des Nachfolgers verdünnt wird.

Voraussetzungen: Sperma verschiedener Männchen gelangt in dieselben Speicherorgane.

Effekt: Der Vaterschaftsanteil des letzten Männchens ist höher als der des Vorgängers.

Bei *C. whitei* gelangt das Sperma aus aufeinanderfolgenden Kopulationen in dieselben Speicherorgane. Eine Verdrängung des Sperma eines Vorgängers aus den Spermatheken hinaus ist auszuschließen, da in den engen Spermathekengängen ein gleichzeitiger Spermatozoentransport in beide Richtungen nicht möglich ist. Daß das Sperma des Vorgängers innerhalb der Spermatheken in eine ungünstige Position verdrängt wird, ist laut Walker (1980) aufgrund ihrer rundlichen Form eher unwahrscheinlich. Für eine Abkapselung von Spermatozoenmengen, wie es bei der Krabbe *Inachus phalangium* (Diesel 1990) beschrieben ist, wurden keine Anzeichen gefunden. Wie sehr sich die Spermatozoen verschiedener Männchen durchmischen, kann nicht beurteilt werden, da dies vom Grad der Spermatozoenbeweglichkeit innerhalb der Spermatheken abhängt. Wenn Durchmischung stattfindet, wird das in den Spermatheken verbliebene Sperma durch neu aufgenommenes verdünnt. Dann sinkt der Vaterschaftsanteil eines Männchens graduell mit jeder nachfolgenden Kopulation des Weibchens.

Im Bereich des ventralen Receptaculum könnte Spermakonkurrenz in der Weise stattfinden, daß aus deformierten oder bereits deplazierten Spermatophoren ausströmende Spermatozoen in das ventrale Receptaculum eindringen. Wenn sie dort gegenüber den regulär aus den Spermathekengängen transferierten Spermatozoen zahlenmäßig überwiegen, resultiert ein Vorteil des zuletzt kopulierenden Männchens bei der Befruchtung der unmittelbar nächsten Eier.

d) Spermatozoenkonkurrenz,

wenn individuelle Spermatozoen um die Befruchtung der Eier konkurrieren.

Voraussetzungen: Sperma verschiedener Männchen gelangt in dieselben Speicherorgane.

Effekt: Der Vaterschaftsanteil ist unabhängig von der Reihenfolge der Kopulationen und von äußerlichen „Qualitätsmerkmalen" des Männchens.

Ob die Spermatozoen von *C. whitei* innerhalb der Spermatheken konkurrieren, hängt von ihrer Fortbewegungsfähigkeit innerhalb dieser Organe ab, die man bisher nicht einschätzen kann. Im Bereich des ventralen Receptaculum wäre die Möglichkeit zur Spermatozoenkonkurrenz gegeben, indem das Spermatozoon das Ei befruchtet, welches aus einer etwa gleichwertigen Ausgangsposition am schnellsten die Strecke bis zur Mikropyle zurücklegt (Diskussion 1. 2). Außerdem könnte beim Eindringen der Spermatozoen in das ventrale Receptaculum im Bereich des Cuticulaborstenfeldes eine Auslese stattfinden.

Auch Konkurrenz unter den Spermatozoen eines einzigen Männchens ist denkbar (Mulcahy 1975). Allerdings wird eine Einflußnahme des Spermatozoengenoms auf den Spermatozoenphänotyp vom Männchen weitgehend unterdrückt (Sivinsky 1984), da agressive Konkurrenz unter den eigenen Spermatozoen sich negativ auf seine Nachkommenzahl auswirken würde.

1.5. Abschließende Einschätzung des Fortpflanzungsverhaltens von *C. whitei*

Walker (1980) schlägt verschiedene Gründe für mehrfache Kopulationen bei weiblichen Insekten vor, die hier auf ihr Zutreffen bei *C. whitei* geprüft werden sollen:

1. Auffüllen des Spermavorrats:

Die Abschätzung in Teil 1.1 hat gezeigt, daß mehrere Kopulationen notwendig sind, um die ca. 2000 Eier zu befruchten, die ein Weibchen im Laufe seines Lebens legen kann. Allerdings läßt sich dadurch keine Kopulationshäufigkeit erklären, bei der das Verhältnis von Kopulationen zu Eiablagen größer als 1 ist.

2. Indirekte Investition des Männchens:

a. Übertragung von Nährstoffen auf das Weibchen:
Die Spermatophoren enthalten einen beträchtlichen Anteil an akzessorischen Sekreten, die auch in die Spermathekengänge transferiert werden. Es ist jedoch noch nicht geklärt, ob diese Investition des Männchens der Ernährung des Weibchens oder der Spermatozoen dient oder eine andere Funktion hat.

b. Erhöhter Schutz vor Prädatoren:
Ein erhöhter Schutz des Weibchens vor Räubern scheint kein plausibler Grund, da das Paar in der Regel nur sehr kurze Zeit zusammen bleibt. (Allerdings ist über die Abwehrmechanismen der Diopsiden ebensowenig bekannt wie über ihre Feinde.)

3. Reduktion des Zeit- und Energieverlusts durch männliche Belästigungen:

Verhaltensbeobachtungen zufolge scheinen abgewiesene Männchen keine ernsthafte Belästigung für Weibchen darzustellen. Außerdem versuchen Männchen nach einer Kopulation oft erneut zu kopulieren, so daß ein Weibchen durch Erdulden einer Kopulation seine Situation nicht verbessern würde.

4. Genetische Gründe:

a. Größere genetische Diversität unter den Nachkommen:
C. whitei ist kein an bestimmte Ressourcen angepaßter Spezialist. Die Eier werden an verrottendes Pflanzenmaterial gelegt, der Lebensraum an Bachufern im tropischen Regenwald ist witterungsbedingt starken Veränderungen unterworfen. Eine hohe genetische Diversität der Nachkommen erhöht einerseits die Chancen, daß zumindest ein Teil der Nachkommen an die jeweiligen Bedingungen besser angepaßt ist, und erniedrigt andererseits die Konkurrenz unter den Nachkommen, da diese verschiedene Ressourcen nutzen können. Allerdings sollen nach Walker (1980) schon die Kopulationen mit einigen wenigen Männchen ausreichen, um das Weibchen mit nahezu dem gesamten Spektrum der genetischen Diversität der Population zu versorgen.

b. Genetische Überlegenheit des zuletzt kopulierenden Männchens:
Um diesen Punkt nicht auf „sperm displacement" zu beschränken, soll dieser Punkt hier so interpretiert werden, daß durch Spermakonkurrenz im weiteren Sinne ein genetisch überlegenes Männchen zum Vater der Nachkommen wird. Hierzu sind bei *C. whi-*

tei mehrere Möglichkeiten gegeben, die schon unter 1.4 der Diskussion abgehandelt wurden.

Für die hohe Kopulationshäufigkeit bei *C. whitei*-Weibchen kommen also im wesentlichen drei der von Walker (1980) vorgeschlagenen Gründe in Betracht: Daß (1) die von den Männchen übertragenen akzessorischen Sekrete dem Weibchen oder seinen Nachkommen zugute kommen, daß (2) aufgrund der hohen Promiskuität einerseits eine hohe genetische Diversität der Nachkommen gewährleistet ist, und daß (3) andererseits im Weibchen Spermakonkurrenz (im engen oder weiteren Sinne) stattfindet.

2. Vergleichende Aspekte des Reproduktionssystems von *C. whitei*

Bisher wurden die weiblichen Geschlechtsorgane bei Überlegungen zur Phylogenie der Dipteren praktisch außer acht gelassen, während die männlichen Geschlechtsorgane eine wesentliche Rolle spielen (z. B.: Griffiths 1972). Dies liegt vermutlich einerseits daran, daß die sklerotisierten Teile der äußeren männlichen Geschlechtsorgane leichter zugänglich und durch Mazeration zu präparieren sind. Andererseits ist hier seitens der Taxonomen schon reichlich Vorarbeit geleistet worden, da gerade diese Organe morphologische Merkmale zur Artunterscheidung auf Gattungsebene bieten.

Die Aufklärung der Phylogenie der acalyptraten Schizophora kommt jedoch mit den bisher verwendeten Merkmalen nurmehr schleppend voran (Griffiths 1972, Hennig 1973, Steyskal 1974, McAlpine 1989, Griffiths 1990). Bei der Bildung von Familiengruppen ist man von einem Konsens noch weit entfernt, aber auch der Status der „Acalyptrata" als monophyletische Gruppe ist bis heute umstritten. Griffiths (1990) entkräftet die von McAlpine (1989) für den Grundplan der Acalyptrata angeführten Apomorphien bis auf die zwei, die das innere weibliche Reproduktionssystem betreffen: 1) zwei von drei Spermatheken an einem gemeinsamen Gang und 2) ein ventrales Receptaculum. Und auch diese zwei Merkmale werden, ihren Wert als Autapomorphie der Acalyptrata betreffend, von Griffiths in Frage gestellt. Die vorliegende Untersuchung und das in Zusammenhang damit angestellte Literaturstudium erlauben eine Einschätzung der Eignung von Merkmalen der inneren weiblichen Geschlechtsorgane, namentlich der Spermatheken, des ventralen Receptaculum und der Vagina für derartige phylogenetische Überlegungen. Außerdem wird diskutiert, inwieweit das Auftreten einer Spermatophore in diesem Zusammenhang Hinweise erbringen kann.

2.1 Spermatheken

Die Hoffnung, daß Form und Anzahl der Spermatheken bei den Schizophora manchen wichtigen Hinweis auf phylogenetische Verwandtschaftsbeziehungen liefern könnten (Hennig 1958), hat sich bis heute nicht erfüllt, obwohl die Literatur zahlreiche Befunde dazu enthält. Wohl aufgrund ihrer meist starken Sklerotisierung sind gerade die Spermatheken der Teil der inneren weiblichen Geschlechtsorgane, der am häufigsten (leider meist als einziger) abgebildet oder beschrieben wurde. Es zeigt sich aber, daß die Spermatheken in ihrer Anzahl und Form einer starken, bisher vom funktionellen Aspekt her ungeklärten Divergenz und Konvergenz unterliegen.

Tab.2: Anzahl der Spermatheken (0, 1, 2, 3, 4) und Vorkommen eines ventralen Receptaculum (vR) bzw. einer Spermatophore (Sp) in den Familien der Diptera. Das System der Nematocera und aschizen Brachycera entspricht mit leichten Veränderungen dem von Steyskal (1974), das der Schizophora folgt McAlpine (1989).

Überfamilie	Familie	0	1	2	3	4	vR	Sp	Qellenangabe
Nematocera									
Tipuloidea	Tipulidae				●				1, 2, 3
	Trichoceridae				●				4
Psychodoidea	Psychodidae	●	●	●					4, 9, 54
	Nymphomyiidae								
Tanyderoidea	Tanyderidae								
	Ptychopteridae								
Blephariceroidea	Blephariceridae			●	●				4
	Deuterophlebiidae								
Culicoidea	Dixidae		●						4
	Chaoboridae		●		●				4
	Culicidae		●	●	●				2, 9
Chironomoidea	Thaumaleidae								
	Simuliidae		●					●	2, 4, 9, 52
	Ceratopogonidae		●	●	●			●	4, 6, 11, 12
	Chironomidae			●	●			●	2, 4, 13
Pachyneuroidea	Pachyneuridae								
	Perissommatidae								
Bibionoidea	Bibionidae		●	●	●			●	2, 3, 4, 5, 6, 7
	Anisopodidae		●	●	●				4
	Mycetophilidae				●				1, 2, 4
	Cecidomyiidae	●	●	●					4, 8
Brachycera									
Xylophagoidea	Xylophagidae					●			14
Stratiomyoidea	Stratiomyidae				●	●			1, 2, 3, 14
	Xylomyidae				●				14
Tabanoidea	Tabanidae					●			1, 2, 3, 9
	Pelecorhynchidae					●			4
	Rhagionidae					●			2, 4
Nemestrinoidea	Nemestrinidae				●				4
	Acroceridae								
	Bombyliidae					●			1, 2, 3, 15, 16
Asiloidea	Asilidae				●	●			1, 2, 3, 18, 19, 20
	Therevidae				●	●			2, 4
	Scenopinidae				●				1, 2
	Mydidae					●			17
	Apioceridae					●			4

Überfamilie	Familie	0	1	2	3	4	vR	Sp	Qellenangabe
Empidoidea	Empididae		•						1, 2, 3, 14
	Dolichopodidae		•						1, 2, 4
Lonchopteroidea	Lonchopteridae			•					2, 56
Phoroidea	Phoridae		•	•					2, 21, 56
	Sciadoceridae								
	Ironomyiidae								
Platypezoidea	Platypezidae				•				2, 56
Syrphoidea	Syrphidae				•				1, 2, 3, 22, 56
	Pipunculidae				•				23, 56

| Σ Nematocera + aschize Brachycera (44 Familien): | | 2 | 12 | 17 | 22 | 0 | | | |

Schizophora

Überfamilie	Familie	0	1	2	3	4	vR	Sp	Qellenangabe
Nerioidea	Micropezidae		•	•			•		2, 14, 56, 59
	Neriidae				•				14, 56
	Cypselomatidae			•					14, 56
Diopsoidea	Tanypezidae		•	•			•		14, 24, 56
	Strongylophthal- myiidae		•				•		14, 56
	Somatiidae								
	Psilidae	•		•			•		2, 14, 24, 56
	Nothybidae		•	•					14
	Megamerinidae		•				•		14, 58
	Syringogastridae				•				14
	Diopsidae		•	•	•		•	•	2, 25, 26, 56
Conopoidea	Conopidae		•		•				2, 14, 56
Tephritoidea	Lonchaeidae		•	•			•		2, 3, 27, 28, 56
	Otitidae		•	•	•		•		1, 2, 3, 28, 29, 56
	Platystomatidae		•	•			•		1, 2, 28, 61
	Tephritidae		•	•			•		28, 30, 31, 32, 56
	Pyrgotidae		•						56
	Tachiniscidae								
	Richardiidae		•						56
	Pallopteridae		•	•					56
	Piophilidae	•	•				•		2, 28, 56
Lauxanioidea	Lauxaniidae		•	•	•		•		2, 14, 28, 33, 34, 56
	Eurychoromyiidae				•				56
	Celyphidae		•						60
	Chamaemyiidae			•	•				2, 24, 28, 56

Überfamilie	Familie	0	1	2	3	4	vR	Sp	Qellenangabe
Sciomyzoidea	Coelopidae				●				2, 3, 56
	Dryomyzidae			●	●				35, 56
	Helosciomyzidae								
	Sciomyzidae			●	●				1, 2, 3, 56
	Ropalomeridae			●	●				56
	Sepsidae			●				●	2, 3, 24, 36, 56
Opomyzoidea	Clusiidae			●				●	2, 56
	Acartophthalmidae								
	Odiniidae			●				●	2, 56
	Agromyzidae			●				●	2, 28, 35, 56
	Fergusoninidae								
	Opomyzidae			●					2, 28, 56
	Anthomyzidae			●				●	2, 28, 56
	Aulacigastridae			●	●			●	2, 56
	Periscelididae				●			●	2, 56
	Neurochaetidae								
	Teratomyzidae								
	Xenasteiidae								
	Asteiidae			●				●	56
Carnoidea	Australimyzidae								
	Braulidae		●						14, 56
	Carnidae	●		●					56
	Tethinidae			●				●	2, 28, 56
	Canacidae			●					2, 28, 56
	Milichiidae			●				●	2, 56
	Risidae								
	Cryptochaetidae		●	●				●	2, 28, 38, 56
	Chloropidae			●				●	2, 39, 40, 56
Sphaeroceroidea	Heleomyzidae			●	●	●		●	2, 3, 56
	Trixocelididae				●				2, 56
	Rhinotoridae			●					56
	Mormotomydiidae								
	Chyromyidae			●					28, 56
	Sphaeroceridae			●	●			●	2, 3, 28, 56, 57
Ephydroidea	Curtonotidae			●	●				56
	Camillidae			●				●	56
	Drosophilidae			●	●			●	2, 3, 41, 42, 43, 56
	Diastatidae			●				●	2, 56
	Ephydridae			●				●	2, 56
Σ acalyptrate Schizophora (64 Familien)		2	4	44	22	9	30		

Überfamilie	Familie	0	1	2	3	4	vR	Sp	Qellenangabe
Calyptrata									
Hippoboscoidea	Glossinidae			•				•	3, 53, 55
	Hippoboscidae			•	•				44
	Streblidae			•					44
	Nycteribiidae			•					44
Muscoidea	Scatophagidae				•				56
	Anthomyiidae				•				3, 45, 46, 56
	Fanniidae								
	Muscidae		•	•	•				2, 3, 47, 56
Oestroidea	Calliphoridae				•	•			1, 48, 56
	Mystacinobiidae								
	Sarcophagidae				•				1, 48, 50, 56
	Rhinophoridae				•				56
	Tachinidae			•	•				1, 51, 56
	Oestridae			•	•				2, 3, 56
Σ Calyptrata (14 Familien)		0	1	7	9	1			
Σ Schizophora (78 Familien)		2	5	51	31	10			
Σ Diptera insgesamt (122 Familien)		4	17	68	53	10			

Quellenangaben: **1** Dufour (1851); **2** Sturtevant (1925, 1926); **3** Wesché (1906); **4** McAlpine et al. (eds.) (1981) (die Autoren der einzelnen Kapitel sind nicht gesondert aufgeführt); **5** Leppla et al. (1975); **6** Linley (1981 a); **7** eigene Untersuchung an *Dilophus febrilis* ergab Vorkommen von 2 Spermatheken und Spermatophore; **8** Metcalfe (1933); **9** Imms (1977); **10** Cook (1965); **11** Wirth & Williams (1954); **12** Pomeranzew (1932); **13** Nielsen (1959); **14** McAlpine & Wood (eds.) (1989) (die Autoren der einzelnen Kapitel sind nicht gesondert aufgeführt); **15** Mühlenberg (1970); **16** Theodor (1983); **17** Jahn (1930); **18** Owsley (1946); **19** Reichhard (1929); **20** Theodor (1976); **21** Disney & Kistner (1990); **22** Gilbert (1986); **23** Harris (1966); **24** Hennig (1958); **25** Feijen (1989); **26** eigene Untersuchung an *Cyrtodiopsis whitei* ergab Vorkommen von 3 Spermatheken, ventralem Receptaculum und Spermatophore; **27** McAlpine (1960); **28** Hardy (1980); **29** Klostermeyer & Anderson (1976); **30** Dodson (1978); **31** Kobayashi (1934); **32** Petri (1910); **33** Oelerich (mündliche Mitteilung, 1990); **34** Yarom (1990); **35** Otronen & Siva-Jothy (1991); **36** eigene Untersuchung an *Sepsis* spec. ergab Vorkommen von 2 Spermatheken und ventralem Receptaculum; **37** Melis (1935); **38** Thorpe (1934); **39** Schwartz (1965); **40** Adams & Mulla (1967); **41** Nonidez (1920); **42** Miller (1965); **43** Shorrocks (1972); **44** Ulrich (1963); **45** Bremer & Kaufmann (1931); **46** Steyskal (1969); **47** Tulloch (1906); **48** Smith et al. (1988); **49** Brat & Chaudhry (1971); **50** Abasa (1972); **51** Leydig (1867); **52** Davies (1965); **53** Pollock (1970); **54** Hennig (1973); **55** Kokwaro et al. (1981); **56** McAlpine et al. (ed.) (1987) (die Autoren der einzelnen Kapitel sind nicht gesondert aufgeführt); **57** Lachmann (mündliche Mitteilung, 1992); **58** eigene Untersuchung an *Megamerina dolium* ergab Vorkommen von 2 Spermatheken und ventralem Receptaculum; **59** eigene Untersuchung an *Mimegralla* spec. ergab Vorkommen von 2 Spermatheken an einem Gang und ventralem Receptaculum; **60** eigene Untersuchung an *Spaniocelyphus umzundusia* ergab Vorkommen von 2 Spermatheken; **61** eigene Untersuchung an *Traphera apicalis* ergab Vorkommen von 2 Spermatheken und ventralem Receptaculum.

Verschiedene Autoren halten drei Spermatheken für ein Grundbauplanmerkmal der Diptera als Ganzes (Downes 1968, Hennig 1973), oder einzelner Teilgruppen der Diptera (Acalyptrata (McAlpine 1989), Cyclorrhapha (Griffiths 1990)). Hennig (1958) schränkte jedoch selbst ein, daß es für seine Annahme von 3 Spermatheken für den Grundbauplan der Schizophora keine hinreichende Begründung gebe. Ein häufig verwendetes Argument ist, daß die Spermathekendreizahl in der entsprechenden Dipterengruppe am häufigsten gefunden wird. Nach dem im Rahmen dieser Untersuchungen angestellten Literaturstudium kommen zwei Spermatheken in sehr viel mehr Familien der Acalyptrata vor als drei (Tab.2). Auch bei den restlichen Dipteren (Nematocera + aschize Brachycera[5]), Calyptrata) kommen drei Spermatheken nur wenig häufiger vor als zwei. Eine Gruppierung in Zusammenhang mit den aktuellen Überfamilien (Steyskal 1974, McAlpine 1989) läßt sich nicht erkennen.

Auf der anderen Seite kommen oft innerhalb einer Familie oder sogar Gattung verschiedene Spermathekenzahlen vor (Tab.2). So haben nach Feijen (1989) Diopsiden in der Regel 3 Spermatheken an 2 Gängen. In den Gattungen *Diasemopsis*, *Chaetodiopsis*, *Trichodiopsis* und *Cobiopsis* gibt es aber nur 2 Spermatheken an je einem Gang, und bei einer Art von *Cladodiopsis* hängt eine kleine vierte Spermathek an dem Gang, der auch die verdoppelte Spermathek trägt (Feijen 1989). Auch innerhalb der Gattung *Cyrtodiopsis* gibt es laut Tan (1965) eine Ausnahme, *Cyrtodiopsis quinqueguttata*, die nur 2 Spermatheken besitzt.

Eine innerartliche Variabilität der Spermathekenzahl von 2—3 ist bei *Drosophila melanogaster* beschrieben (Miller 1965, Shorrocks 1972). Während bei *C. whitei* mit bisher nur einer Ausnahme immer der rechte Spermathekengang zwei Spermatheken trägt, kann die gepaarte Spermathek bei *Tetanops myopaeformis*, *Drosophila melanogaster* und *Psila lateralis* links oder rechts vorkommen (Klostermeyer & Anderson 1976).

Nicht viel anders sieht es mit der Spermathekenform aus. Bei den Diopsiden sind sowohl bedornte Formen als auch glatte, runde Formen bekannt, mit oder ohne ins Lumen hineinragenden Gangansatz (Tan 1965, Feijen 1989). Eine noch viel stärkere innerfamiliäre Vielfalt der Spermathekenformen wurde zum Beispiel bei Asilidae (Theodor 1976), Bombyliidae (Mühlenberg 1970, Theodor 1983) und Pipunculidae (Harris 1966) beschrieben. Innerhalb dieser Familien reicht das Spektrum von mehr oder weniger runden Formen mit und ohne Eindellung bis hin zu extrem tubulären.

Aus diesen Befunden geht hervor, daß die Spermatheken mit ihrer starken Veränderlichkeit ein eher ungeeignetes Merkmal darstellen, um die verwandschaftlichen Zusammenhänge der Diptera auf höherer taxonomischer Ebene zu untersuchen.

2.2 Ventrales Receptaculum

Einige Autoren halten es für möglich, daß das ventrale Receptaculum eine Autapomorphie der Acalyptrata darstellt (Hennig 1973, McAlpine 1989). Tatsächlich ist bei vielen

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[5]) Als „aschize Brachycera" wird hier der paraphyletische Rest bezeichnet, der von den Brachyceren nach Ausschluß der Schizophora übrigbleibt. Er umfaßt die vermutlich ebenfalls paraphyletischen „Brachycera Orthorrhapha" und „Cyclorrhapha Aschiza". Auch für die „Nematocera" gilt Paraphylie als wahrscheinlich.

Acalyptrata, und nur dort, ein ventrales Receptaculum bekannt (Tab.2), jedoch leider nur in wenigen Fällen genauer beschrieben. Es ist nur selten ersichtlich, inwieweit die verschiedenen Bezeichnungen, „ventrales Receptaculum", „Befruchtungskammer", „Bursa copulatrix", etc., der verschiedenen Autoren homologe, funktionell vergleichbare, oder in Struktur und Funktion völlig verschiedene Organe bezeichnen.
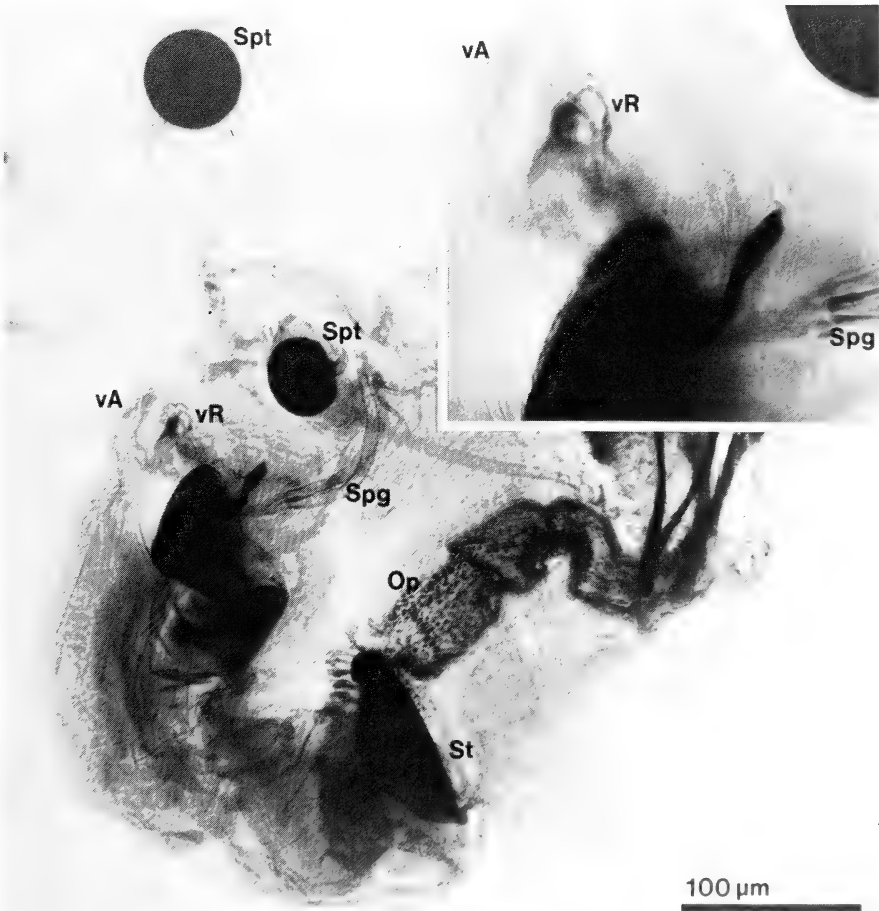
Abb.45: Innere weibliche Geschlechtsorgane von *Sepsis* spec. (Sepsidae), Totalpräparat in Polyvinyllacto-phenol mit Direkttiefschwarz. Lateralansicht von links; Einsatz: craniale Region der Vagina.

Op: Ovipositor, Spg: Spermathekengänge, Spt: Spermathek, St: Stilett, vA: ventrale Aussackung, vR: ventrales Receptaculum.

Dem ventralen Receptaculum von *C. whitei* in Lage, Funktion, und gekammerter Struktur entsprechende Organe sind bei einigen Tephritidae („ventral receptacle" bei *Rhagoletis pomonella* (Dean 1935), „morula gland" bei *Strumeta tryoni* (Drew 1968), „fertilization chamber" bei *Dacus oleae* (Solinas & Nuzzaci 1984)) und Otitidae („ventral receptacle" bei *Tetanops myopaeformis* (Klostermeyer & Anderson 1976)) beschrieben. Eigene Untersuchungen erbrachten darüberhinaus ähnliche Befunde bei weiteren Tephritidae und bei Sepsidae. Bei den von mir untersuchten Arten *C. whitei*, *Ceratitis capitata*, *Rhagoletis cerasi* und *Sepsis* spec. (Abb.45) umfaßt die morphologische Ähnlichkeit dickwandige, jedoch nicht sklerotisierte, rundliche Cuticulakammern in gefächerter Anordnung sowie das Vorkommen von Cuticulaborstenfeldern im zuführenden Gang. Es scheint zunächst unwahrscheinlich, daß es sich hierbei um mehrfache Konvergenz handelt.

Caudal des gekammerten ventralen Receptaculum besitzt *Sepsis* eine weitere, dünnwandige Aussackung (Abb.45), die ihre Entsprechung bei *C. whitei* in einer an gleicher Stelle gelegenen, relativ unauffälligen Falte findet (ventrale Aussackung, Kap. „Vagina"). Die ventrale Bursa copulatrix von *Tetanops myopaeformis* (Klostermeyer & Anderson 1976) hingegen dürfte hier für eine Homologie nicht in Frage kommen, da sie caudal von der verdickten Intima des „Sacculus" (Diskussion 2.3) inseriert.

Die Beantwortung der Frage, ob und mit welcher dieser Strukturen die ventralen Receptacula anderer Acalyptrata, etwa das tubuläre, dünnwandige ventrale Receptaculum von *Drosophila melanogaster* (Nonidez 1920, Miller 1965) oder das einkammrige, stark sklerotisierte ventrale Receptaculum der Ephydridae (Sturtevant 1926), homolog sind, könnte zu wertvollen Hinweisen auf die Verwandtschaft der Acalyptrata führen.

Bei den Calyptrata findet sich ein dem ventralen Receptaculum von *C. whitei* in Lage und Funktion entsprechendes Organ in der Befruchtungskammer von *Musca domestica* („fertilization chamber", Leopold et al. 1978). Das Dach dieser Befruchtungskammer trägt innen hexagonal angeordnete Cuticuladornen, deren Basen durch Stege verbunden sind. Denkt man sich diese Stege an den Dornen entlang emporgewachsen, so kommt man zu Cuticulakammern, deren Trennwände in Cuticuladornen auslaufen, wie es bei *C. whitei* der Fall ist. Auch im ventralen cranialen Bereich der Vaginae von *Calliphora erythrocephala* (Graham-Smith 1938) und *Glossina austeni* (Pollock 1974) sind mit Cuticuladornen versehene Bereiche beschrieben. Sollten die genannten Strukturen mit dem ventralen Receptaculum von *C. whitei* homolog sein, so wäre dadurch der Status des ventralen Receptaculum als mögliche Autapomorphie der Acalyptrata (McAlpine 1989) stark in Frage gestellt. Hier sind Vergleiche mit weiteren Calyptrata und mit verschiedenen aschizen Brachycera unerläßlich.

2.3 Vagina

Aufgrund der vorliegenden morphologischen und funktionellen Befunde kann ein Homologisierungsvorschlag für die verschiedenen Vaginabereiche von *C. whitei* mit denen anderer bereits gut untersuchter Dipterenarten vorgelegt werden:

a) Der caudal vom sklerotisierten Ring gelegene Teil der „Vagina" von *C. whitei* (Definition s. dort) dürfte dem bei *Calliphora erythrocephala* (Brüel 1897, Graham-Smith 1938) als „Vagina" bezeichneten Bereich der Genitalkammer entsprechen. Die verglichenen Bereiche besitzen keine Ringmuskulatur, werden bei der Kopulation mehr oder weniger aus der Vulva hervorgestülpt, und werden durch dorsal und ventral ansetzende Muskelzüge in die Ruhelage zurückgezogen. Bei *Sepsis punctum* könnte dieser Bereich dem handschuhfingerartig hervorstülpbaren Ovipositor (Kiontke 1989) entsprechen, an dem ebenfalls dorsal und ventral ansetzende Muskelzüge gefunden wurden. Auch bei *Drosophila melanogaster* ist der caudale Teil der Vagina frei von Ringmuskulatur (Miller 1965), und *Drosophila caputidis* besitzt einen hervorstülpbaren Oviprovector (Grimaldi 1976), der obiger Region entsprechen könnte.

b) Der restliche Teil der Vagina von *C. whitei*, von ihrem cranialen Ende bis zum caudalen Ende des sklerotisierten Ringes, kann dementsprechend mit dem oft als „Uterus" bezeichneten cranialen Teil der Genitalkammer von *Calliphora* und *Drosophila* verglichen werden. Er ist in allen Fällen mit einer starken Ringmuskulatur versehen. Schwierigkeiten bei der Homologisierung scheinen zunächst die paarigen dorsalen Uterustaschen von *Calliphora* zu bereiten. Glücklicherweise hat jedoch Brüel (1897) die Ontogenese dieser Taschen detailliert untersucht: Sie gehen aus zwei Spalten hervor, die einen großen dorsalen Vorsprung zwischen der Genitalpapille und der Vulva lateral begrenzen, und die später größtenteils geschlossen werden. Dieser dorsale Vorsprung in Brüels Beschreibung ist der dorsalen medianen Falte bei *C. whitei* sehr ähnlich, so daß hier eine Homologie zumindest denkbar ist.

Bei *C. whitei* und einigen anderen Dipterenarten liegt in diesem cranialen Teil der Vagina ventral eine mehr oder weniger starke Sklerotisierung vor, deren Vorhandensein und Form sich besonders für einen Vergleich anbietet. Bei *C. whitei* hat diese Sklerotisierung die Form eines längsovalen Ringes, an dem ein wesentlicher Teil der Vaginamuskulatur inseriert. Ringförmige Sklerite in dieser Region sind auch bei Canacidae (Wirth 1989) und den Phoridae (Brown 1988) beschrieben. Bei *Tetanops myopaeformis* (Otitidae) erscheint die Intima des cranialen Teils der Vagina („Sacculus") ventral braun sklerotisiert (Klostermeyer & Anderson 1976). Bei *Sepsis punctum* liegt ein als „Stilett" bezeichnetes Sklerit in der ventralen Wand der Vagina, welches bei hervorgestülptem Ovipositor dessen caudale Begrenzung bildet (Kiontke 1989), ähnlich der Hinterkante des sklerotisierten Ringes von *C. whitei* bei der Kopulation. Auch bei *Calliphora erythrocephala* sind in der ventrolateralen Wand der Vagina Sklerotisierungen ausgebildet, die diese im hervorgestülpten Zustand während der Kopulation stützen (Graham-Smith 1938). Diese sind jedoch in ihrer Lage relativ zur Vaginamuskulatur nicht mit dem sklerotisierten Ring von *C. whitei* zu vergleichen.

Eine vergleichende Untersuchung der Vaginae darf sich nicht auf die Morphologie von sklerotisierten Strukturen beschränken, sondern muß die Muskulatur und die Funktion der entsprechenden Teile, beispielsweise die Ausstülpbarkeit der Vagina bzw. die Ausbildung eines Ovipositors mit einbeziehen. Sie könnte möglicherweise sowohl ausreichend Gemeinsamkeiten als auch Unterschiede aufweisen, um für phylogenetische Betrachtungen gerade auf der Ebene höherer Taxa von Bedeutung zu sein.

2.4 Spermatophore

Spermatophoren werden von vielen Autoren als ein primitives Merkmal der Insecta eingestuft (Khalifa 1949, Davey 1960, Hinton 1964, Alexander 1964). Ihr Vorkommen ist in fast allen Insektenordnungen beschrieben (Tabelle 3). In vielen Ordnungen kommen jedoch neben spermatophorenbildenden Arten auch solche vor, die freies Sperma übertragen, ja manchmal ist dieser Unterschied schon bei nahe verwandten Arten zu verzeichnen (Khalifa 1949). Dies ließe sich durch eine mehrfache konvergente Reduktion der Spermatophore erklären, oder auch durch deren konvergente Neuentwicklung.

Lange Zeit wurde angenommen, daß die relativ „hochentwickelten" Antliophora (Siphonaptera + Mecoptera + Diptera) die Spermatophorenbildung ganz aufgegeben hätten, zugunsten der Übertragung von freiem Sperma (Hennig 1973). Spermatophorenfunde bei einigen Nematocera (Ceratopogonidae (Pomeranzew 1932), Simuliidae (Rubzow 1959) Chironomidae (Nielsen 1959) und möglicherweise Thaumaleidae (Downes 1968)) und der Mecoptere *Boreus westwoodi* (Mickoleit 1974) wurden als konvergente Neuentwicklungen gedeutet. Der „mating plug" von *Anopheles gambiae* wurde von Giglioli (1966) als evolutionärer Vorgänger oder Überrest einer Spermatophore interpretiert.

1970 beschrieb Pollock die erste Spermatophore einer calyptraten Brachycere (*Glossina austeni*). 1972 fügte er die Spermatophore einer Bibionide (*Plecia nearctica*) hinzu und diskutierte Spermatophoren als ein primitives Merkmal der Diptera (Pollock 1972,

Tab.3: Vorkommen von Spermatophoren (Sp) bei den Insecta. ● steht für bisher erbrachte Nachweise, ? steht für einen noch fraglichen Nachweis.

Ordnung	Sp	Quellenangabe	Ordnung	Sp	Quellenangabe
Collembola	●	1,3,7	Psocoptera	●	1,2,3,7
Protura			Phthiraptera	●	1,3
Diplura	●	1,3	Hemiptera	●	1,2,3,7
Archaeognatha	●	1,3	Thysanoptera	?	1
Zygentoma	●	1,3	Strepsiptera		
Ephemeroptera	●	1	Coleoptera	●	1,2,3,7
Odonata	●	1,2	Rhaphidioptera	●	3
Plecoptera	●	4	Megaloptera	●	3
Embioptera	●	3	Neuroptera	●	1,2,3,7
Phasmida	●	1,2,3	Hymenoptera	●	1,2,3,5,7
Orthoptera	●	1,2,3,5,7	Trichoptera	●	1,2,3,7
Grylloblattaria			Lepidoptera	●	1,2,3,7
Dermaptera	●	7	Mecoptera	●	1,6
Dictyoptera	●	1,2,3,7	Siphonaptera		
Zoraptera			Diptera	●	1,2,3,7

Quellenangaben: **1** Mann (1984); **2** Gerber (1970); **3** Tuzet (1977); **4** Zwick (1980); **5** Davey (1960); **6** Mickoleit (1974); **7** Thornhill (1976b).
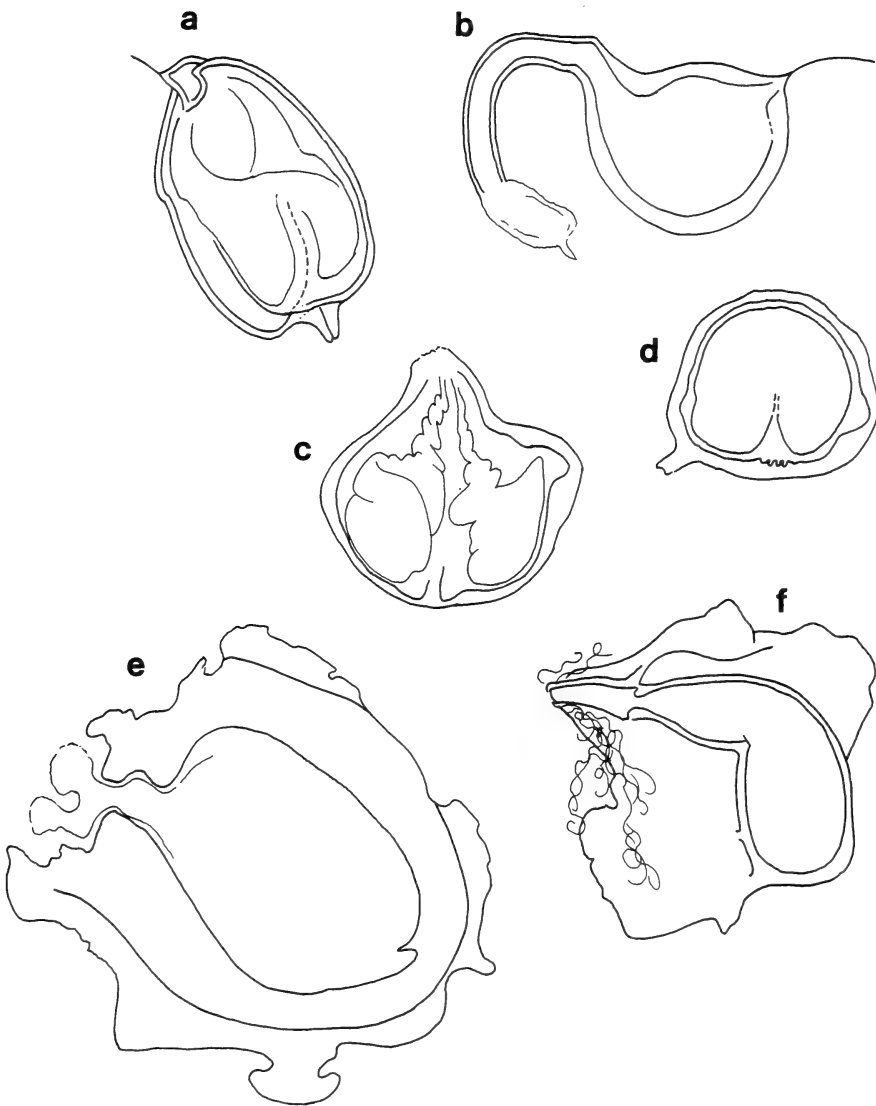
Abb.46: Spermatophoren von verschiedenen Dipteren. (a) *Dilophus febrilis* (Bibionidae), eigene Untersuchung; (b) *Culicoides melleus* (Ceratopogonidae) nach Linley & Adams (1971); (c) *Glyptotendipes paripes* (Chironomidae) nach Nielsen (1959); (d) *Simulium salopiense* (Simuliidae) nach Davies (1965); (e) *Glossina morsitans* (Glossinidae) nach Kokwaro et al. (1981); (f) *Cyrtodiopsis whitei* (Diopsidae), eigene Untersuchung.

1974). Er nahm an, daß auch bei anderen Brachycera letztendlich Spermatophoren gefunden würden.

Die Erwähnung einer Spermatophore von *Drosophila melanogaster* (Fowler 1973 zitiert in diesem Zusammenhang fälschlicherweise Hinton 1963, die Aussage geht aber offensichtlich auf DeVries 1964 zurück) wurde inzwischen widerlegt (Gromko et al. 1984). Die Entdeckung der Spermatophore von *C. whitei* scheint jedoch nunmehr für Pollocks Annahme zu sprechen. Derzeit sind Spermatophoren in zwei verschiedenen Entwicklungslinien der Nematocera und in jeweils einer Familie der acalyptraten und der calyptraten Brachycera bekannt (Tab.2 und 4). Da die Schwestergruppen der Cyclorrhapha und der Brachycera nicht bekannt sind, lassen sich aus dieser Verteilung keine phylogenetischen Schlußfolgerungen ziehen. Wenn jedoch die Spermatophore von *Boreus westwoodi* mit berücksichtigt wird, scheint die Frage, ob und wie oft Spermatophoren innerhalb der Antliophora konvergent neu entstanden sind, doch berechtigt.

Pollock (1972) wies darauf hin, daß bisher kein gesicherter Fall einer Spermatophorenneuentwicklung bekannt ist. Hingegen ist die konvergente Reduktion der Spermatophore innerhalb mehrerer Insektenordnungen zu verzeichnen. Der Übergang von der vom Männchen vorgeformten Spermatophore zur erst innerhalb der weiblichen Geschlechtsorgane geformten Spermatophore und weiter zur direkten Übertragung flüssigen Spermas in die weiblichen Receptacula wird allgemein als evolutive Höherentwicklung angesehen (Gerber 1970, Khalifa 1949, Parker 1970, Weidner 1982, Mann 1984).

Die verschiedenen Spermatophoren der Diptera lassen sich hypothetisch in eine derartige Entwicklungsreihe einordnen, wenn auch betont werden muß, daß ihre eventuelle Homologie bisher völlig ungeklärt ist. Während bei den spermatophorenbildenden Nematocera die Spermatophore ganz oder teilweise außerhalb des Weibchens verbleibt, wird sie bei den beiden spermatophorenbildenen Brachycera im cranialen Teil der Vagina abgesetzt (Tab.4). Diese Verlagerung entspricht der obigen Entwicklungsrichtung. Sie könnte gleichzeitig mit der evolutiven Verlagerung der Mündung der Spermathekengänge nach innen einhergegangen sein. Bei den Nematocera wird die Spermatophore mehr oder weniger im paarigen Anfangsteil des Ductus ejaculatorius der Männchen vorgeformt und durch einen relativ weiten Ductus ejaculatorius ohne Spermapumpe übertragen (Linley 1981a). Daß die fertige Spermatophore ein Verschmelzungsprodukt aus ursprünglich zwei Spermakammern ist, läßt sich manchmal noch an ihrer Form erkennen. Bei *C. whitei* hingegen werden verschiedene Sekrete nacheinander durch einen wesentlich schmäleren Ductus ejaculatorius mittels einer Spermapumpe in die Vagina des Weibchens übertragen, wo eine einkammerige Spermatophore entsteht. Bei *Glossina austeni* liegen widersprüchliche Befunde vor: Laut Pollock (1972) wird die Spermatophore erst im Weibchen geformt, während Tibayrenc & Itard (1970) angeben, daß die Spermatophore im Männchen vorgeformt wird. Die von Pollock (1974) bei *Glossina austeni* als „ejaculatory pump" bezeichnete Struktur ist ein Teil des Aedeagus und nicht mit der Spermapumpe von *C. whitei* homolog. Bei *Glossina pallidipes* ist der innerartliche Wechsel von der Spermatophorenbildung zur Übertragung freien Spermas beschrieben, wobei es sich um eine alternative Strategie handeln soll, für den Fall, daß

Tab.4: Vergleichende Zusammenstellung aus der Literatur verfügbarer Befunde über Spermatophoren bei Dipteren.

Familie	Bibionidae	Ceratopogonidae	Chironomidae	Simuliidae	Diopsidae	Glossinidae
Art	Plecia nearctica	Culicoides melleus	Glyptotendipes paripes	Simulium salopiense	Cyrtodiopsis whitei	Glossina austeni
Autor	Leppla 1975	Linley 1981a, 1981b	Nielsen 1959	Davies 1965	Kotrba 1990	Pollock 1970, 1974
Kopulationsdauer	56 h[1]	10 min	3—5 s	2—3 min 75 s[3]	45 s	2—24h
Spermatransfer in die Spermatheken	ca. 1—12,5 h nach Kopulationsbeginn	4—6 min nach Kopulationsbeginn	ca. 5—20 min nach Kopulationsbeginn	ca. 4—55 min nach Kopulationsbeginn[3]	ca. 1—30 min nach Kopulationsbeginn	ca. 1—24 h nach Kopulationsbeginn
Bildung der Spermatophore		Im Männchen vorgeformt			Nicht im Männchen vorgeformt[4]	Im Männchen vorgeformt
Positionierung der Spermatophore	Verbleibt größtenteils in den Genitalien des Männchens, wird nur teilweise in das Weibchen eingeführt		An der Mündung der Spermathekengänge, ragt teilweise aus der weiblichen Geschlechtsöffnung heraus		An der Mündung der Spermathekengänge, im cranialen Teil der Vagina	
Schicksal der Spermatophore	Bleibt am Männchen, wird kurz nach der Trennung abgeworfen	Bleibt am Männchen oder wird vom Weibchen innerhalb 40 s nach der Trennung abgeworfen		Wird vom Weibchen einige Zeit nach der Trennung abgeworfen	Wird vom Weibchen innerhalb 1 h nach der Trennung ausgeschieden	Wird vom Weibchen innerhalb ca. 24 h nach der Trennung ausgeschieden
Spermakammer	Eine Kammer, teilweise unterteilt	Eine Kammer (aus zwei Kammern verschmolzen)	Zwei Kammern mit getrenntem Ausgang	Eine Kammer, teilweise unterteilt	Eine Kammer, auch nicht teilweise unterteilt	
Wand der Spermatophore	Einschichtig			Mehrschichtig	Mehrschichtig	Mehrschichtig
Inhalt der Spermatophore	Spermatozoen in zwei Bündeln angeordnet(?)/"granular spermatozoa"	Spermatozoen in zwei Spiralen angeordnet + granuläres Material	Spermatozoen in zwei Spiralen angeordnet	parallel angeordnete Spermatozoen + granuläres Material	locker angeordnete, teils aufgerollte Spermatozoen + stark anfärbbare Tröpfchen	dicht gepackte Spermatozoen + "darkly staining masses"

Befunde, von anderen Autoren bzw. Arten als im Tabellenkopf angegeben, sind durch hochgestellte Zahlen gekennzeichnet: **1** (Thornhill 1976a); **2** *Dilophus febrilis* (eigene Untersuchung); **3** *Simulium decorum* (Linley & Simmons 1983); **4** Bei *Glossina austeni* widersprüchliche Befunde: laut Pollock (1974) im Weibchen geformt, laut Tibayrenc & Itard (1970) im Männchen vorgeformt.

kein akzessorisches Drüsensekret zur Verfügung steht (Jaenson 1979). Es wäre denkbar, daß hier der letzte Schritt der Spermatophorenreduktion nach dem oben genannten Schema erreicht ist.

Es gibt bereits aus anderen Familien der Acalyptrata Befunde, die auf das Vorkommen von mehr oder weniger reduzierten Spermatophoren hinweisen könnten. So wurde sowohl bei *Sepsis punctum* (Kiontke 1989) als auch bei *Dryomyza anilis* (Otronen 1991) beschrieben, daß die in der Vagina abgesetzte Spermamenge von einer Gallerte bzw. durchsichtigen Flüssigkeit umgeben ist. Weitere Untersuchungen der Spermatophoren der Diptera könnten interessante Ergebnisse erbringen: Etwa Hinweise auf einen Selektionsdruck, unter dem Spermatophoren mehrfach konvergent entwickelt wurden, oder vielleicht die Einstufung der Spermatophore als ursprüngliches Merkmal der Diptera.

2.5 Abschließende Einschätzung der Eignung von Merkmalen der inneren weiblichen Geschlechtsorgane und der Spermatophore für vergleichende Untersuchungen zur Klärung höherer Verwandtschaftsbeziehungen

Die äußeren männlichen Geschlechtsorgane der Insekten unterliegen meist einer starken Divergenz und werden deshalb von Taxonomen gerne zur Artbestimmung herangezogen, während sie zur Klärung übergeordneter Verwandschaftsbeziehungen eher ungeeignet sind. Im Gegensatz dazu ist die Divergenz der inneren weiblichen Geschlechtsorgane der Insekten im allgemeinen weit geringer (Eberhard 1985). In den vorangegangenen Kapiteln wurden einige Merkmale der inneren weiblichen Geschlechtsorgane der höheren Dipteren diskutiert, die für den Vergleich auf der Ebene höherer Taxa geeignet erscheinen. Besonders im Bereich des ventralen Receptaculum bestehen auf Familienniveau in Lage, Form und Struktur ausreichend Gemeinsamkeiten und Unterschiede, um eine Klärung von Verwandtschaftsverhältnissen zu erhoffen. Ähnliches gilt für den hervorstülpbaren Teil der Vagina und die Sklerotisierung in der ventralen Vaginawand. Hingegen erweist sich gerade das Merkmal, das bisher am häufigsten beschrieben wurde, die Spermathekenzahl, als eher ungeeignet für derartige Untersuchungen. Sie variiert innerhalb der Familien und Gattungen (Tab.2), ja teilweise sogar innerhalb einer Art. Ob das Vorkommen von Spermatophoren für phylogenetische Überlegungen ein aussagekräftiges Merkmal darstellen kann, werden erst zukünftige Untersuchungen zeigen.

Über die systematische Stellung der Diopsidae herrscht noch Uneinigkeit. Sie werden von verschiedenen Autoren (Hennig 1958, Prado 1969, McAlpine 1989) in die nähere Verwandtschaft der Syringogastridae, Megamerinidae, Nothybidae, Psilidae, Somatiidae, Strongylophthalmyiidae und Tanypezidae gestellt (Tabelle 2), während Griffiths (1972, 1990) diese Gruppe für heterogen hält. Leider liegen bisher aus keiner weiteren Familie dieser Gruppe ausreichend Befunde über die inneren Geschlechtsorgane der Weibchen vor, um eine Stellungnahme zu ermöglichen. In der weiteren Verwandtschaft (Nerioidea, Conopoidea und Tephritoidea (McAlpine 1989)) ist nur der Vergleich mit einigen Tephritoidea (Dean (1935), Klostermeier & Anderson (1976), Solinas & Nuzzaci (1984)) möglich, der bemerkenswerte Ähnlichkeiten im Bereich des ventralen Receptaculum ergibt (s.o.). Diese Ähnlichkeiten werden aber auch mit den Sepsidae (eigene

Untersuchung) geteilt. Während aus dem von McAlpine (1989) vorgeschlagenen System keine nähere Verwandtschaft der Diopsidae mit den Sepsidae erkennbar ist, hält es Griffiths (1989) für möglich, daß beide Familien den Sciomyzoidea zuzuordnen sind. In diesem Zusammenhang könnte auch von Bedeutung sein, daß der Ovipositor der Sepsidae (handschuhfingerartige Ausstülpung der Vagina) viel eher als der der Tephritidae (letzte Abdominalsegmente modifiziert) bei *C. whitei* seine Entsprechung findet (Diskussion 2.3).

Noch sind keine neuen Aussagen über die Verwandtschaftsverhältnisse der Diopsidae und der anderen Acalyptrata möglich. Doch scheint die Untersuchung der inneren weiblichen Geschlechtsorgane weiterer acalyptrater Familien in dieser Richtung vielversprechend.

ZUSAMMENFASSUNG

Die Morphologie der männlichen und weiblichen Geschlechtsorgane, Eier und Spermatozoen von *Cyrtodiopsis whitei* wurde mit herkömmlichen Methoden licht- und elektronenmikroskopisch untersucht, unter besonderer Berücksichtigung der inneren weiblichen Geschlechtsorgane. Anhand von Verhaltensbeobachtungen und der Präparation von in entsprechenden Verhaltenskontexten fixierten Tieren konnten außerdem die inneren Vorgänge bei der Kopulation und der Eiablage weitgehend rekonstruiert werden.

Die inneren weiblichen Geschlechtsorgane von *C. whitei* umfassen paarige, meroistisch polytrophe Ovarien, die lateralen Ovidukte und den Oviductus communis, eine muskulöse Vagina, drei Spermatheken an zwei Gängen, ein Paar akzessorische Drüsen und schließlich ein gekammertes ventrales Receptaculum, welches vorher bei den Diopsidae noch nicht beschrieben war. In der ventralen Wand der Vagina ist ein sklerotisierter Ring ausgebildet, an dem Ring- und Längmuskulatur der Vagina inserieren, so daß ein besonders differenziertes Epithelpolster in seiner Mitte von der Muskelschicht ausgespart bleibt. In der dorsalen Wand der Vagina wurde auf Höhe des sklerotisierten Ringes durch $CoCl_2$-Füllung ein transversaler Nervenplexus nachgewiesen, der möglicherweise einen Dehnungsrezeptor darstellt.

Als Resultat der Untersuchung von während oder kurz nach der Kopulation fixierten *C. whitei*-Weibchen konnte erstmals der Transfer von Sperma mittels einer Spermatophore bei einer acalyptraten Diptere nachgewiesen werden. Die einkammerige, keulenförmige Spermatophore wird vom Männchen während der nur 45 s dauernden Kopulation im cranialen Teil der weiblichen Vagina gebildet. Aus der Spermatophore werden anschließend Spermatozoen und akzessorische Sekrete in die Spermatheken des Weibchens entleert. Von dort gelangen die fadenförmigen Spermatozoen später ins ventrale Receptaculum, an dessen Mündung die Besamung der Eier stattfindet.

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Die Ergebnisse werden in ihrer Bedeutung für das Fortpflanzungsgeschehen von *C. whitei* diskutiert und mit Befunden aus der Literatur verglichen. Die Funktion des gekammerten ventralen Receptaculum und der Spermatophore wird erörtert, mögliche Gründe für die hohe Kopulationszahl und Promiskuität der Weibchen und verschiedene Möglichkeiten der Spermakonkurrenz werden aufgezeigt. Schließlich wird die mögliche Bedeutung von Merkmalen der inneren weiblichen Geschlechtsorgane für zukünftige phylogenetische Untersuchungen diskutiert.

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Anatomie und Phylogenie der Bibionomorpha
(Insecta, Diptera)

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INHALT

EINLEITUNG

Seit Hennig (1950) die Grundzüge einer Theorie der Phylogenetischen Systematik entwickelt hat, ist eine beachtliche Zahl an Arbeiten über die Stammesgeschichte der Diptera (Insecta, Holometabola) veröffentlicht worden. Dennoch zeigen neuere Zusammenstellungen (Hackman & Väisanen 1982, Krivosheina 1989, Wood 1989) Lücken und Kontroversen in der Begründung verwandtschaftlicher Zusammenhänge innerhalb der Diptera; das gilt sogar für die Differenzierung der Großgruppen.

In konventionellen Klassifikationen werden den sicher monophyletischen Brachycera (= Fliegen) die Nematocera (= Mücken) gegenübergestellt. Unter Berücksichtigung aller Hypothesen zur Stammesgeschichte der Diptera zeigt sich allerdings, daß bislang kein Autor die Nematocera der Klassifikation als monophyletische Gruppe begründen konnte, so daß sich hinter diesem Namen vermutlich eine paraphyletische Rest-Gruppe verbirgt — im Sinne eines Konglomerats aller „Nicht-Brachycera". Bei der Lösung dieses Problems spielt eine Teilgruppe der nematoceren Diptera, die Bibionomorpha, eine besondere Rolle. Verschiedene Autoren halten es für wahrscheinlich, daß die Bibionomorpha als Schwestergruppe der Brachycera zu gelten haben (Colless & McAlpine 1970; Hackman & Väisanen 1982; Hennig 1968, 1981; Rohdendorf 1974; Steyskal 1974). Begründet wird dieses postulierte Schwestergruppen-Verhältnis — wenn überhaupt — mit Übereinstimmungen im Bau des Thorax. Diese Hypothese über die Existenz einer von Bibionomorpha + Brachycera gebildeten geschlossenen Abstammungsgemeinschaft kann erst dann überprüft und besser belegt werden, wenn das Grundmuster der Bibionomorpha für weitere Merkmalskomplexe rekonstruiert worden ist.

Die Bibionomorpha sensu Hennig (1954, 1973) sind eine umfangreiche Gruppe, zu der folgende Taxa gehören: Anisopodidae, Perissommatidae, Pachyneuridae (mit Cramptonomyiidae), Axymyiidae, „Hyperoscelidae", Scatopsidae, Bibionidae, Mycetophilidae, Sciaridae und Cecidomyiidae.

Die Monophylie dieser Gruppierung kann aber nicht befriedigend belegt werden; nach Hennig (1973: 30) kann nur eine Autapomorphie im Flügelgeäder als Argument angeführt werden. Diese Schwierigkeit läßt sich darauf zurückführen, daß Merkmalsausprägungen im Flügelgeäder in den Mittelpunkt phylogenetischer Forschung gestellt und Widersprüche, die sich aus der Berücksichtigung anderer Merkmalskomplexe ergeben haben, nicht diskutiert worden sind. So ist die Analyse des Flügelgeäders (Hennig 1954) und die daraus resultierende Gruppierung der Bibionomorpha niemals einhellig anerkannt worden. Dies betrifft vor allem die Stellung der kleineren Taxa Pachyneuridae, Cramptonomyiidae, Axymyiidae, Anisopodidae und Scatopsoidea (Tuomikoski 1961, Rohdendorf 1974, Krivosheina 1989). Es gibt sogar eine ältere, aber durchaus begründete Alternative zur Stellung der Anisopodidae und Scatopsoidea (Bischoff 1922; Keilin & Tate 1940); diese sind aufgrund einer synapomorphen Übereinstimmung der larvalen Mandibel (zweigeteilt) näher mit den Trichoceridae verwandt als mit den übrigen Bibionomorpha. Wood (1989: 1350) bestätigt diese Auffassung, und auch in der vorliegenden Arbeit wird dieser Hypothese der Vorzug gegeben.

Eine weitere Schwierigkeit entsteht durch Informationsmangel. Dies betrifft die artenarmen Perissommatidae, deren Larvenstadien bislang unbekannt geblieben sind, und auch die Axymyiidae. Es scheint gerechtfertigt, diese beiden (kleinen) Taxa aus der Analyse der verwandtschaftlichen Beziehungen solange auszuklammern, bis ausreichend Material für die Bearbeitung mehrerer Merkmalskomplexe zur Verfügung steht.

6

Somit verbleiben als Bibionomorpha die Pachyneuridae, Cramptonomyiidae, Bibioni-
dae, Cecidomyiidae, Sciaridae und Mycetophilidae („Pilzmücken" im weitesten Sinn).
Diese Taxa werden in der vorliegenden Arbeit einer Analyse gemäß der Methodik der
Phylogenetischen Systematik unterzogen. Dafür werden besonders Merkmale aus dem
Komplex der männlichen und weiblichen Terminalia herangezogen, aber auch Thorax
und Extremitäten finden Beachtung. Neben dem Versuch einer Neu-Bewertung bekann-
ter, einseitig gewählter Merkmale ist vor allem die Ermittlung und Analyse möglichst
weit gefächerter neuer Ergebnisse als tragfähige Grundlage für die Rekonstruktion ver-
wandtschaftlicher Beziehungen anzusehen.

Für die praktische Arbeit ist die große Diversität der Bibionomorpha ein besonderes
Problem. Die z.T. sehr hohen Artenzahlen verschiedener Familien (vgl. Abb.1) schließen
eine Berücksichtung aller Arten im Rahmen einer Dissertation natürlich aus. Das ist
aber auch nicht notwendig, denn in vielen Gruppen wird ein vorliegendes Merkmals-
muster kaum variiert.

Die Prinzipien der Phylogenetischen Systematik (Hennig) werden als theoretische Basis
der Untersuchung herangezogen. Der im Mittelpunkt dieser Methodik stehende Außen-
gruppen-Vergleich umfaßt als engere Außengruppe die Diptera excl. Bibionomorpha
und als weitere Außengruppe Mecoptera, Siphonaptera und manchmal noch die
Amphiesmenoptera (Lepidoptera + Trichoptera).

Ziel der vorliegenden Arbeit ist es, das Grundmuster der Bibionomorpha zu rekonstru-
ieren. Auf dieser Grundlage sind, soweit möglich, Schwestergruppen-Verhältnisse inner-
halb der Bibionomorpha zu belegen. Darauf fußend kann die Frage nach der Stellung
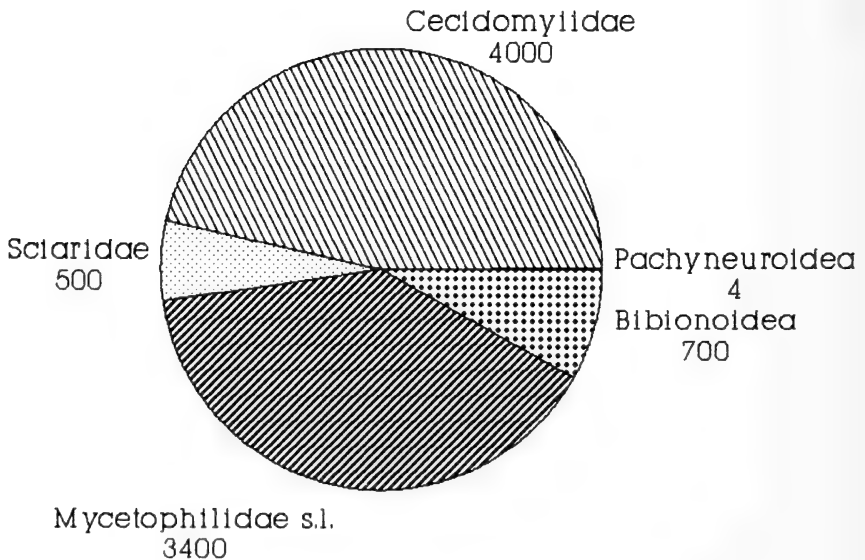
Abb. 1: Diversität (Artenzahl) der Bibionomorpha, verteilt auf die höheren Taxa der Klassifikation.

der Bibionomorpha im System der Diptera diskutiert sowie zum „Nematoceren-Problem" Stellung genommen werden.

MATERIAL UND METHODE

Für die Untersuchung verschiedener Merkmalskomplexe sind folgende Arten aus fast allen höheren Taxa (Familien der konventionellen Klassifikation) berücksichtigt worden. Wenn nicht anders angegeben, lagen jeweils mehrere Individuen beider Geschlechter vor.

Bibionidae
Pleciinae
    Penthetria funebris Meigen, 1804; [BER]
    Plecia ornaticornis Skuse, 1899; [COL]
    P. amplipennis Skuse, 1889; [COL]
Bibioninae
    Dilophus febrilis (Linnaeus, 1758); [BER]
    Bibio leucopterus (Meigen, 1804); [BER]
    B. marci (Linnaeus, 1758); [BER]

Cecidomyiidae
Lestremiinae
    Campylomyza flavipes Meigen, 1818; [BER]

Sciaridae
    Sciara thomae (Linnaeus, 1767); [BER]
    Trichosia trochanterata (Zetterstedt, 1851); [BER]
    Lycoriella mali (Fitch, 1856); [BER]
    Caenosciara alnicola (Tuomikoski, 1957); [BER]
    Bradysia amoena (Winnertz, 1867); [BER]
    B. paupera Tuomikoski, 1960; [BER]

Diadocidiidae
    Diadocidia ferruginosa (Meigen, 1830); [SMF, 610, 611; ZSM, 12.064]

Mycetophilidae
Ditomyiinae
    Australosymmerus fuscinervis (Edwards, 1921); [COL]; (1,0)
    A. nebulosus Colless, 1970; [COL]; (1,1)
    A. aculeatus (Edwards, 1921); [COL]; (0,1)
    Symmerus annulatus (Meigen, 1830); [ZSM; 10.302, 11.924]
    Ditomyia fasciata (Meigen, 1818); [BER; SMF]
Bolitophilinae
    Bolitophila glabrata Loew, 1869; [SMF; 1957, 1944]
    Bolitophila tenella Winnertz, 1863; [SMF, 605]
Keroplatinae
    Keroplatus testaceus (Dalman, 1818); [BER]
    Platyura marginata Meigen, 1804; [SMF; 2068, 1069. ZSM; 10. 576, 20838]
    P. harrisi Tonnoir, 1927; [BMNH]
    Neoplatyura flava (Macquart, 1826); [SMF]
    Macrocera maculata Meigen, 1818 [BER]

Sciophilinae
Mycomyia bicolor (Dziedzicki, 1885); [SMF]
Azana anomala (Staeger, 1840); [BER]
Sciophila rufa Meigen, 1830; [SMF; BER]
S. hirta Meigen, 1818; [BER]
Boletina trivittata (Meigen, 1818); [SMF, 716]
Leia winthemi Lehmann, 1822; [SMF, 730]
Rondaniella dimidiata (Meigen, 1804); [SMF]

Mycetophilinae
Mycetophila fungorum (de Geer, 1776); [SMF, 5060; BER]
M. strigata Staeger, 1840; [BER]
Phronia biarcuata (Becker, 1908); [SMF, 8159]; (0,1)
Anatella spec. [SMF, 7345]; (0,3)
Cordyla brevicornis (Staeger, 1840); [BER]
Exechia confinis Winnertz, 1863; [BER]
E. seriata (Meigen, 1830); [BER]

Präparation

Das Material lag meistens in Alkohol fixiert und konserviert vor, in selteneren Fällen erfolgte eine Fixierung in Bouin'schen Gemisch (modifiziert nach Gregory).

Die Kleinheit der Tiere machte in aller Regel eine mikroskopische Untersuchung notwendig. Für die Bearbeitung des Exoskeletts wurden die betreffenden Objekte in Hoyer's Gemisch eingebettet. Zur Untersuchung von Muskulatur und anderen Weichteilen sind die Objekte erst in Boraxkarmin gefärbt (Stückfärbung) und dann in Euparal eingebettet worden. Es hat sich bewährt, dunkel pigmentierte Stücke zuvor mit 15% H_2O_2 zu bleichen.

Lückenlose Schnittserien im Semidünn-Bereich (0,5—2 µm) vertieften das Verständnis komplexer Strukturen. Material aus eigenen Aufsammlungen wurde zu diesem Zweck mit dem modifizierten Bouin'schen Gemisch (nach Gregory) fixiert; Material aus den Sammlungen der Museen stand lediglich in Alkohol fixiert zur Verfügung. Dieser Umstand schloß eine detaillierte Untersuchung der Histologie aus.

Alle Objekte sind aus 96% Alkohol direkt in LR WHITE (soft grade), ein Acrylharz der London Resin Company, überführt worden. Zur Polymerisation wurden 10 ml LR WHITE mit 1 Tropfen Beschleuniger versetzt, in Kunststoff-Förmchen (Deckel von Rollrand-Gläsern) gefüllt und das Objekt ausgerichtet. Das Förmchen wurde mit einem weiteren Deckel möglichst luftdicht abgeschlossen und im Wasserbad bei Zimmertemperatur 2 Stunden gekühlt. Große Objekte, die nicht in die flachen Kunststoff-Förmchen paßten, sind in Gelatinekapseln eingeblockt worden. In diesen Fällen polymerisierte das LR WHITE ohne Beschleuniger bei 60 °C im Wärmeschrank (12 Stunden).

Zum Schneiden stand ein Mikrotom der Firma Reichert (AUTOCUT) zur Verfügung. Verwendet wurden ausschließlich Glasmesser, die damit erzielte Schnittdicke lag zwischen 0,5 µm und 2 µm. Die Schnitte wurden nicht, wie in der Produktinformation der London Resin Company angegeben, mit 40% Aceton auf Objektträger aufgezogen, sondern lediglich mit aqua bidest. bei 60 °C—70 °C aufgetrocknet.

Die Färbung der Schnitte erfolgte mit Toluidinblau in Natriumbicarbonat-Lösung. Nach dem Trocknen auf der Wärmeplatte bei 60 °C wurden die Objektträger kurz in

Xylol gestellt; die Schnitte sind dann, noch tropfnass, in Entellan eingeschlossen worden.

Die lichtmikroskopische Untersuchung erfolgte mit einem LEITZ Mikroskop der Serie DIALUX (Hellfeld und Differential-Interferenzkontrast). Für die Dokumentation der Präparate stand ein Zeichenspiegel zur Verfügung. Die genauere Untersuchung von Oberflächen machte den Einsatz der Rasterelektronen-Mikroskopie notwendig. Zur Trocknung wurden die Objekte über eine Aceton-Reihe in Iso-Amylacetat gebracht und dann im critical-point-Verfahren weiterbehandelt. Nach dem Aufkleben mit Kohlekleber sind die Objekte mit Gold bedampft worden. Sämtliche Aufnahmen wurden mit dem Gerät CAMBRIDGE (Serie 4) angefertigt.

Abkürzungen der Sammlungen

BER   Sammlung Berthold, Hamburg
BMNH British Museum (Natural History), London
COL   Sammlung Colless, CSIRO, Canberra
SMF   Senckenberg Museum, Frankfurt a.M.
ZSM   Zoologische Staatssammlung, München

Die in den Abbildungen verwendeten Abkürzungen sind im Text hergeleitet. Eine Liste dieser Abkürzungen befindet sich im Anhang.

VERGLEICHENDE MORPHOLOGIE

Bau und Funktion der männlichen Terminalia

Als Terminalia werden diejenigen Endsegmente des Abdomens bezeichnet, die in ihrer Funktion als Träger von Geschlechts- und Exkretionsorganen eine mehr oder weniger starke Abwandlung erfahren haben (s. Kèler 1955: „Terminalia"). Hierbei handelt es sich bei den Dipteren — wie bei den Ectognatha generell — um die abdominalen Segmente IX—XI, die zusammen diesen Funktionskomplex bilden. Der hierfür in der dipterologischen Literatur weitverbreitete Terminus „Hypopygium" wird hier nicht verwendet, weil er bei nematoceren Diptera und Brachycera verschiedene Strukturen bezeichnet (Matsuda 1976: 348).

Zum besseren Verständnis und zur Vereinfachung des deskriptiven Teils der vorliegenden Arbeit wird als erstes die Terminologie wesentlicher Strukturelemente des männlichen Terminalkomplexes erörtert werden.

Gonopoden: An der Extremitäten-Natur der zweigliedrigen äußeren Zangenarme wird heute kaum noch gezweifelt (McAlpine 1981: 51), aber die Unsicherheit bezüglich der Homologisierung mit einzelnen Extremitätenabschnitten drückt sich in der Literatur in einer unterschiedlichen Terminologie für die Zangenarme aus. Zur Verfügung stehen die Begriffspaare (und ihre Varianten) „Gonocoxit (Coxit, Gonocoxopodit, Coxopodit) — Gonostylus" und „Basistylus — Dististylus"; die auf Crampton (1942) — der die Gonopodennatur der äußeren Zangenarme anzweifelte — zurückgehenden und von Snodgrass (1957) aufgegriffenen Bezeichnungen „Basimer — Telomer" haben sich nicht durchsetzen können.

Um die bestehende Verwirrung in der Terminologie nicht noch weiter zu vergrößern, soll in der vorliegenden Arbeit einzig und allein aus Gründen der Zweckmäßigkeit den Begriffen „Gonocoxit — Gonostylus" der Vorzug gegeben werden. Diese werden in Bearbeitungen verschiedener Taxa häufig benutzt und auch im neuesten — englischsprachigen — Überblick über die Morphologie der Diptera verwendet (McAlpine 1981: 51).

Als **Genitalkammer** wird in der vorliegenden Arbeit der Bereich bezeichnet, der zwischen den Medialflächen der Gonocoxite eingeschlossen ist.

Phallisches Organ: Das unpaare, median zwischen den Gonopoden liegende Begattungsorgan (vgl. Fig.6, 24) ist eine Bildung der Genitalhöhle, die aus der weit craniad eingestülpten Conjunctiva des 9. und 10. Segmentes entsteht (Snodgrass 1935: 582); dies hat zur Folge, daß das Begattungsorgan sowohl mit dem Analkomplex als auch mit den ventralen Teilen des Exoskeletts über eine Membran verbunden ist.

Nach Matsuda (1976: 71) ist von der Vielzahl der Termini, mit denen das männliche Begattungsorgan belegt wird, der Begriff „Penis" in seiner Definition der umfassendste, da er auch paarige und sogar nicht penetrierende Strukturen einschließt. Deswegen wird dieser Terminus hier vor allen anderen (Phallus, Aedoeagus) bevorzugt.

Parameren: Die paarigen, ungegliederten Anhänge, die medial zwischen den Gonopoden an der Paramerenbasis (Dorsalbrücke, pons parameralis, dorsal bridge) entspringen (vgl. Fig.59) und innerhalb der Diptera sehr häufig zu finden sind (McAlpine 1981: 51),

werden meist als Parameren bezeichnet (Hennig 1973: 212; van Emden & Hennig 1956). Die durch diese Benennung implizierte Homologie dieser Parameren mit ebenso bezeichneten Gebilden in anderen Insektengruppen muß aber als unsicher gelten (s. auch Tuxen 1956: „Parameres"), so daß diese Begriffswahl nicht besonders glücklich erscheint. Da es sich aber bei dem Begriff „Parameren" gerade um einen der wenigen handelt, die konsequent und einheitlich von Bearbeitern verschiedener Dipteren-Taxa benutzt werden, wäre die Einführung einer neuen Bezeichnung wohl sehr verwirrend und stünde kaum in Einklang mit den Bestrebungen, ein einheitlicheres Begriffsinventar zu schaffen; so soll hier das betreffende Spangenpaar im Rahmen der Tradition weiterhin als Parameren bezeichnet werden.

Muskulatur: Im allgemeinen wird die Muskulatur des Postabdomens ihrer Funktion nach in Gruppen eingeordnet und getrennt beschrieben. Diesem Prinzip wird auch hier gefolgt werden; betrachtet werden die Muskeln des Begattungsorgans und die Bewegungsmuskulatur der Gonostyli. Auf eine funktionell-anatomische Benennung der Muskeln wird in der vorliegenden Arbeit (mit zwei Ausnahmen) verzichtet; sie werden einzeln durchnumeriert, wobei Homologa die gleiche Nummer erhalten. Diese Vorgehensweise ermöglicht die tabellarische Zusammenfassung der Ergebnisse mit denen anderer Autoren und erleichtert so die Vergleichbarkeit der Muskelausstattung in verschiedenen Taxa.

Spermatransfer: Wegen der engen Verknüpfung von Struktur und Funktion werden im deskriptiven Teil der Arbeit auch Beobachtungen zum Modus der Spermaübertragung aufgeführt, auch wenn solche Daten nur für sehr wenige der untersuchten Arten zur Verfügung stehen.

Die folgende Darstellung der männlichen Terminalia berücksichtigt Vertreter sowohl der Bibioniformia (Bibionidae) als auch der Mycetophiliformia. In die Untersuchung der artenreichen Mycetophiliformia konnten fast alle höheren Taxa der konventionellen Klassifikation (Familien bzw. Unterfamilien) einbezogen werden.

Bibionidae

1. *Penthetria funebris* Meigen, 1804

Exoskelett
Die 8 prägenitalen Segmente sind mit ihren Terga und Sterna deutlich ausgebildet. Auf sie folgt der Terminalkomplex, der nicht invertiert getragen wird, die morphologische Dorsalseite weist also auch tatsächlich nach oben (Fig.2). Die sieben Stigmenpaare liegen in der Pleuralmembran der Segmente I—VII.

Das Tergum des 9. Segmentes ist groß und bedeckt als Epandrium nicht nur die Basis, sondern auch den größten Teil der Dorsalfläche der Gonocoxite (Fig.3, G). Sein caudaler Rand ist breit eingebuchtet, lateral ist es über eine ausgedehnte Membran mit den Gonocoxiten verbunden. An das Epandrium schließt sich direkt der Analkomplex, bestehend aus dem häutigen Analkegel (AK), den paarigen Cerci (C) und dem ventral liegenden Hypoproct (Hp), an. Sowohl Cerci als auch Hypoproct sind lediglich apikal stärker sklerotisiert, wobei aber die Ausdehnung der sklerotisierten Bereiche einer beträchtlichen intraspezifischen Variabilität unterliegt. Der gesamte Komplex liegt nor-

malerweise soweit unter dem Tergum IX verborgen, daß nur die Spitzen der Cerci erkennbar sind; er kann aber auch weit ausgestülpt werden. Reste des Tergum X, welches — wenn vorhanden — in dem Bereich zwischen Epandrium und Cerci liegen müßte, sind nicht mehr zu identifizieren.

Das Sternum des 9. Segmentes ist als distinktes Element nicht erkennbar. Die Basalglieder der Gonopoden, die Gonocoxite, bilden auf der Ventralseite eine einheitliche Fläche aus, sie sind miteinander verschmolzen und bilden die Ventralfläche des Genitalsegments (Fig.4, B). Dieser Bereich des Genitalkomplexes ist nahezu durchgehend stark sklerotisiert, lediglich am caudalen Rand befindet sich medial eine unpaare, weniger stark sklerotisierte Schwächezone (m). Die deutlich ausgeprägten Gelenkhöcker für die dicondyle Gelenkung zwischen Gonocoxit und Gonostylus werden beide vom Gonocoxit gebildet (Fig.5).

Die Gonostyli sind länger als breit, einteilig zangenartig geformt und im Querschnitt stark abgeflacht; medial ist ihr Rand zu einer subapikalen Spitze ausgezogen.

Nach Entfernen des Epandrium einschließlich des Analkomplexes wird deutlich, daß die Gonocoxite eine Genitalkammer einschließen (Fig.6). Die ventral zu einer unpaaren Platte miteinander verschmolzenen Gonocoxite wölben sich latero-dorsad auf und laufen auf der Dorsalseite jederseits in ein langes, breit löffelförmiges Apodem, das Gonocoxit-Apodem (GA)[1], aus. Caudal wird der Rand des Genitalsegments ebenfalls von den Gonocoxiten gebildet, die dort plattenartig die Kammer begrenzen. Abgesehen vom Epandrium wird der dorsale Abschluß der Genitalkammer von einer sehr dünnen Membran gebildet, die jederseits zwischen dorso-caudalem Rand der Gonocoxite, Gonocoxit-Apodemen und Penis ausgespannt ist.

Penis
Zwischen den paarigen, löffelförmig ausgebildeten Gonocoxit-Apodemen ist der Penis (Fig.6, Pe) eingehängt. Das direkt verbindende Element ist dabei eine weit caudad geschwungene, spitz auslaufende Skleritspange, die Dorsalbrücke (Db). Diese Skleritspange erweitert sich in ein median gelegenes, unpaares Sklerit. Es bildet als Dorsalsklerit (Ds) oder Tegmen die dorsale Bedeckung des Penis. In der Lateralansicht wird deutlich, daß es sich beim Dorsalsklerit um ein dreidimensional kompliziert geformtes Gebilde handelt (Fig.9). In einem weiten Bogen erstreckt sich seine Oberfläche bis zum Ventrum des Penis und ist dort zweizipfelig ausgezogen (Fig.8). Zwischen den Außenrändern dieser Spitzen und dem dorsalen Rand des Tegmen ist eine Lamelle ausgespannt (Fig.8; laterale Lamelle, lL), welche nur sehr schwach sklerotisiert ist. Sie bildet die laterale Wand des Penis. Aber auch median zwischen den paarigen Spitzen des Dorsalsklerits befindet sich eine weitere Lamelle, die direkt in den Ductus ejaculatorius übergeht (Fig.9; dorsale Lamelle, dL)

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[1] Die Linie, entlang welcher das Gonocoxit-Apodem eingefaltet ist, bildet die Grenze zwischen dem eigentlichen Apodem (Hypandriumapodem sensu Ulrich) und dem zugehörigen Sklerit (Hypandriumarm, Ulrich 1974). Sie ist in Totalpräparaten kleiner Objekte schwer zu erkennen, und um ihre Lage und ihren Verlauf bei allen Arten darzustellen, wären weitere Untersuchungen nötig gewesen, die den Rahmen der vorliegenden Arbeit gesprengt hätten. Zum Verständnis der nachfolgenden Beschreibungen und Abbildungen sei deshalb betont, daß der als Gonocoxit-Apodem bezeichnete sklerotisierte Komplex einen Teil der Oberfläche mit einschließen kann.

Im Innern des Penis befindet sich median ein mächtig ausgebildetes, unpaares Apodem (meA), das ebenfalls vom Dorsalsklerit gebildet wird: die medialen, deutlich verstärkten Kanten seiner Dorsalfläche setzen sich ventrad in das Innere des Penis als Apodem fort. Eine weitere Fläche für den Ansatz von Muskeln wird lateral von dem plattenförmig erweiterten cranialen Rand des Dorsalsklerit gebildet (Platten-Apodem, PlA).

Während sowohl der dorsale als auch der laterale Abschluß des Penis vom Dorsalsklerit direkt gebildet werden, begrenzt ein weiteres Sklerit, ein Teil des sogenannten Ejaculator-Apodems (E)[1], das Begattungsorgan auf der Ventralseite. Dieses Apodem (Fig.9) ist basal plattenartig abgeflacht und verbreitert, geht aber weiter apikal in einen weniger stark sklerotisierten, löffelartig ausgehöhlten Bereich (aE) über. Der craniale Rand dieses „Löffels" wird lateral durch eine rechtwinklig zur Apodem-Längsachse stehende Skleritspange abgestützt. Die Dorsalfläche des apikalen Bereichs setzt sich als ventrale Lamelle (vL) craniad in das Innere des Ductus ejaculatorius fort. Ventral ist der Apex des Ejaculator-Apodems über die ausgedehnte, stark aufgefaltete Conjunctiva des 9. Segments mit dem caudalen Rand der Genitalkammer verbunden.

Der durchgehend muskularisierte Ductus ejaculatorius (De) durchzieht den gesamten Penis zwischen Dorsalsklerit und Ejaculator-Apodem (Fig.10). In seinem Endabschnitt wird die Intima deutlich dicker und setzt sich caudad als die bereits weiter oben beschriebenen dorsale und ventrale Lamelle (dL, vL) fort. Der Raum, der von dorsaler und ventraler Lamelle umschlossen wird, kann als Endophallus (Ep) aufgefasst werden. Der primäre Gonoporus liegt im Bereich der Einmündung des Ductus ejaculatorius in den Endophallus. Dieser öffnet sich in einer großen, unpaaren Geschlechtsöffnung, dem Phallotrema (Fig.11, 12, 13; Pt) zwischen Dorsalsklerit und Ejaculator-Apodem am Apex des Penis.

Dorsale und ventrale Lamelle des Endophallus sind mit besonders differenzierten Haaren besetzt; diese sind schuppenartig verbreitert und weisen mehrere Spitzen auf, die ohne Ausnahme caudad weisen (Fig.14, 15).

Innerhalb des Penis befindet sich eine paarige Drüse (Fig.10, 11a, akzessorische Drüse, aD). Diese ist direkt mit dem Ejaculator-Apodem verbunden und mündet in den Endophallus (Fig.11b).

Muskulatur

Die Bewegungsmuskulatur der Gonostyli besteht aus dem kräftig entwickelten Gonostylus-Adduktor (Fig.7, M1) und dem schwächer ausgeprägten Gonostylus-Abduktor (M2). Am cranialen Rand der Ventralwand entspringen die Adduktoren. Dieses Muskelpaar nimmt im Bereich seines Ansatzes nahezu die gesamte Ventralfläche des Genitalsegments ein. Weiter caudad entspringen mehrere seitliche Ausläufer an den lateralen Innenflächen der Gonocoxite. Die distale Insertionsstelle des sich stark verjüngenden Muskels befindet sich an der Medialfläche des Gonostylus.

Der Gonostylus-Abduktor (M2) entspringt dorso-lateral ebenfalls am cranialen Rand des Genitalsegments. Im Gegensatz zum Adduktor bleibt er aber in seiner Ausdehnung auf den lateralen Bereich der Gonocoxite beschränkt und bildet auch keine Nebenmus-

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[1] Als Ejaculator-Apodem wird hier der ganze sklerotisierte Komplex bezeichnet, der teils eingefaltet ist — das eigentliche Apodem —, teils an der Oberfläche liegt und insoweit ein Sklerit bildet.

keln aus. Der Abduktor inseriert auf der Dorsalseite außen direkt an der Basis des Gonostylus an einem kleinen randlichen Vorsprung.

Ein weiteres Muskelpaar (M7) erstreckt sich zwischen der dorsalen Wand der Gonocoxite und den Apodemen derselben. Diese Muskeln dienen vermutlich der Stabilisierung des Genitalsegments.

Zwei Paar Muskeln verbinden den Penis mit dem Exoskelett des Genitalsegments, sie dienen der Bewegung des gesamten Begattungsorganes. Das erste Paar (M11) entspringt an der Ventralseite des Gonocoxit-Apodems und inseriert an der Unterseite des Platten-Apodems des Dorsalsklerits. Der zweite, weit größere Muskel (M4) hat seinen Ursprung auf der Oberfläche der Dorsalbrücke und erstreckt sich caudad weit in das Innere. Dort inseriert er breit an den Innenflächen des caudalen Randes des Segments und des Gonocoxit-Apodems. Bei Kontraktion dieses Muskels wird der gesamte Penis caudad gezogen und dabei senkrecht aufgerichtet, eine Stellung, die während der Kopulation eingenommen wird (vgl. auch Fig.70). Die vielfach aufgefaltete und dadurch stark dehnbare häutige Verbindung zwischen Ejaculator-Apodem und caudalem Rand des Genitalsegments steht in funktionellem Zusammenhang mit dieser Bewegung.

Innerhalb des Penis sind ebenfalls zwei Muskelpaare zu finden. Ein Muskel (M5) verbindet das Dorsalsklerit mit dem Ejaculator-Apodem; er entspringt an der Ventralfläche des Platten-Apodems und inseriert — wiederum an der Ventralseite — des Ejaculator-Apodems. Die Kontraktion dieses Muskelpaares führt zur Retraktion des Apodems, was sich auf die Ausdehnung des Endophallus-Lumens auswirkt und die Größe des Phallotrema verändert. Eine ähnliche Wirkung hat ein weiteres, mächtig entwickeltes Muskelpaar (Fig.10, M3), das seinen Ursprung jederseits des medianen Apodems im Innern des Penis hat. Ursprungsstelle ist direkt die Innenseite des Dorsalsklerits. Der Muskel verläuft dorso-ventral entlang des medianen Apodems bis zur dorsalen Lamelle; an dieser inseriert er auf breiter Fläche. Da diese Lamelle die dorsale Begrenzung des Phallotrema bildet, führt die Kontraktion des Muskelpaares zu einer Erweiterung von Endophallus und Geschlechtsöffnung.

Funktionell gehört auch die aus Ring- und Längsfasern bestehende Muskularis des Ductus ejaculatorius zur Muskulatur des Penis.

Innere Geschlechtsorgane (Fig.69)

Die paarigen, dorso-ventral stark abgeflachten Hoden (Ho) liegen im Dorsum des 5. abdominalen Segmentes. Die ebenfalls paarigen und sehr dünnen Vasa deferentia (Vd) durchziehen das Abdomen bis zum 8. Segment, wo sie sich zu der drüsigen Vesicula seminalis (Ve) erweitern. Direkt an die Vesicula schließt sich der unpaare Ductus ejaculatorius (De) an.

Spermatransfer

Die Männchen von *P. funebris* bilden nachweislich Spermatophoren aus (Fig.16, 70, Spe). Indirekte Hinweise auf diesen Modus des Spermatransfer geben auch die große sekundäre Geschlechtsöffnung (Phallotrema) und besonders Vorhandensein und Ausrichtung der schuppenartigen Haare auf den Innenseiten der Gonoporus-Region: die Spitzen der Haare weisen immer caudad. Eine Spermatophore kann somit leicht in Richtung Geschlechtsöffnung geschoben werden, ein Zurückrutschen wird vermutlich durch die Aufrauhung der Oberfläche in nur einer Richtung verhindert. Während der

Kopulation bleibt die Spermatophore mit dem männlichen Genitale verbunden, so daß sie — funktionell betrachtet — als Element des Penis anzusehen ist.

Die Muskulatur innerhalb des Penis (M3, M5) dient sicherlich dem Transport der Spermatophore innerhalb des Genitaltraktes und ihrer Fixierung während der Kopulation. Die Frage, auf welche Art und Weise das Sperma aus der Spermatophore in die weiblichen Receptacula gelangt, ist noch offen und einer weiteren Untersuchung vorbehalten.

2. *Plecia ornaticornis* Skuse, 1899

Exoskelett

Die praegenitalen Segmente I—VIII sind mit ihren Terga und Sterna vollständig ausgebildet. Der Terminalkomplex wird nicht invertiert getragen, die morphologische Dorsalseite weist nach oben (Fig.18). Es sind sieben Paar abdominaler Stigmen ausgebildet, die in der Pleuralmembran der Segmente I—VII lokalisiert sind.

Das Epandrium (Fig.19, TIX) ist groß, medial aber auffallend tief eingebuchtet; es bedeckt lateral nahezu die gesamte Dorsalfläche der Genitalkammer, erreicht aber nicht deren caudalen Rand. Da das Tergum IX durch die tiefe Einbuchtung medial lediglich als schmale Spange ausgebildet ist, ragt der größte Teil des Analkomplexes, die Cerci (C) und der Hypoproct (Hp), unter seinem caudalen Rand hervor. Weitere Sklerite sind im Bereich des Analkegels nicht vorhanden.

Die Gonocoxite (G) sind ventral vollständig verschmolzen (Fig.20, B); lediglich im caudalen Bereich dieser Platte ist die Cuticula als membranöse Schwächezone (m) ausgebildet. Ein distinkt ausgebildetes Sternum des 9. Segmentes ist nicht vorhanden. Am caudalen Rand sind die Gonocoxite zu mehreren Fortsätzen ausgezogen (Fig.20, 21, 22); die lateralen (lGF) und mediolateralen (mlGF) sind jeweils paarig, der mediane (mGF) aber unpaar ausgebildet. Alle diese Fortsätze sind mit warzenartigen Höckern besetzt (Fig.23).

Die Gonostyli (Gs) sind sehr klein und bis auf ihre Basis reduziert. Ihre Gelenkung ist mediad verschoben, so daß sie ventral der medio-lateralen Gonocoxit-Fortsätze liegen; in voller Größe sind sie nur in Frontalansicht zu erkennen (Fig.21, 22).

Nach Entfernen des Tergum IX zeigt ein Blick auf die Genitalkammer (Fig.24), daß die Gonocoxite am caudalen Rand nicht nur ventral, sondern auch dorsal miteinander verbunden sind; diese dorsale Verbindung geht direkt in den medianen Fortsatz (mGF) über. Dorso-lateral sind von den Gonocoxiten Gonocoxit-Apodeme (GA) abgesetzt, die durch eine halbkreisförmige Platte, die Dorsalbrücke (Db), untereinander in Verbindung stehen. Die Dorsalbrücke ist direkt mit dem Dorsalsklerit (Ds) des Penis verbunden, eine Naht ist aber noch zwischen beiden Elementen sichtbar.

Penis

Zwischen den deutlich ausgebildeten Gonocoxit-Apodemen ist der Penis eingehängt. Das Dorsalsklerit (Fig.26, Ds) erscheint durch Bereiche partieller Desklerotisierung stark differenziert. Auf einen sklerotisierten, direkt an die Dorsalbrücke anschließenden Teil folgt eine membranöse Zone, die sich bis zum caudalen Ende des Penis erstreckt. Durch die Ausbildung dieser „Schwächezone" sind die stark sklerotisierten Seitenwände des Dorsalsklerits als bewegliche, caudad leicht zugespitzte Spangen (dorsale Spangen, dSp) ausgebildet.

Ein weiteres Spangenpaar (ventrale Spangen, vSp) entspringt direkt an den Apodemen der Gonocoxite, erstreckt sich caudad bis zur Penisspitze und ist dort lateral mit dem Ejaculator-Apodem (E) verbunden. Beide Spangenpaare stehen durch eine schwach sklerotisierte Zone miteinander in Verbindung.

Bei *P. amplipennis* (Fig.27) sind die ventralen Spangen (vSp) plattenartig ausgebildet und überragen craniad die Dorsalbrücke (Db), die auch hier deutlich vom Dorsalsklerit (Ds) abgesetzt ist. Die dorsalen Spangen (dSp) sind über eine schmale, membranöse Zone beweglich an den Gonocoxit-Apodemen befestigt. Auch bei dieser Art ist das Dorsalsklerit partiell membranös, aber nicht in dem Ausmaße wie bei *P. ornaticornis*.

Im Innern des Penis ist ein schmales, unpaares Apodem (Fig.26, 27, 28, 31; medianes Apodem, meA) zu erkennen, das an der Ventralseite von Dorsalbrücke und Dorsalsklerit entspringt und das senkrecht zu deren Oberfläche steht. Das mediane Apodem setzt sich caudad bis in die Spitze des stark sklerotisierten Teils des Dorsalsklerits fort. Das Ejaculator-Apodem (Fig.30, 31; E) stellt die ventrale Begrenzung des Penis dar. Im basalen Teil besteht es aus einer einfachen, sklerotisierten Platte, die weiter caudal tief eingeschnitten ist. Der darauf folgende Teil (aE) ist membranös differenziert, setzt sich dorsad fort und bildet einen Teil des Endophallus. Apikal ist das Ejaculator-Apodem durch einen Einschnitt in einen dorsalen und ventralen Teil getrennt. Der ventrale Abschnitt schließt sich über eine Membran (Conjunctiva) direkt an den caudalen Rand des Genitalkammerbodens an. Die horizontale Zweiteilung des Apex dürfte die Flexibilität bei Bewegungen in dorso-ventraler Richtung deutlich erhöhen.

Der Ductus ejaculatorius (De) mündet in einen Hohlraum, den Endophallus (Fig.32, Ep). Die Wände des Endophallus werden von einer Lamelle gebildet, die dorsal (dorsale Lamelle, dL) mit dem Dorsalsklerit und ventral (ventrale Lamelle, vL) mit dem Ejaculator-Apodem verbunden ist. Der primäre Gonoporus (pG) ist in der ventralen Lamelle lokalisiert. Die sekundäre Geschlechtsöffnung, das Phallotrema (Pt), ist sehr groß und liegt an der Spitze des Penis zwischen Dorsalsklerit und Ejaculator-Apodem.

Muskulatur
Obwohl die Gonostyli in ihrer Größe stark reduziert sind, ist ihre Bewegungsmuskulatur mächtig entwickelt. Ein Muskelpaar (Fig.25; M1) entspringt breit am cranialen Rand der Ventralwand des Genitalsegments und inseriert an der dorsalen Innenkante des Gonostylus (Fig.21).

Das andere, viel kleiner ausgebildete Paar (M2) entspringt an der Seitenwand des Genitalsegments, verläuft immer schmaler werdend ventrad und inseriert schließlich an der ventralen Außenkante des Stylus (Fig.21).

In ihrer Funktion sind beide Muskeln wohl kaum noch als einfache Ad- bzw. Abduktoren zu verstehen, auch scheint die Greiffunktion der stark verkürzten Gonostyli fraglich. Aber aufgrund der Lage, besonders ihres Ursprungsortes, lassen sich beide Muskelpaare eindeutig mit M1 und M2 der übrigen Bibionidae homologisieren.

Der Penis steht mit dem Genitalsegment über drei Muskelpaare in Verbindung. Das erste Paar (Fig.25, 33; M4) entspringt dorso-lateral an der Wand des Genitalsegments und inseriert an den ventralen Spangen des Dorsalsklerits nahe ihrer Verbindungsstelle mit dem Gonocoxit-Apodem. Antagonistisch zu diesen Muskeln wirkt ein Paar (Fig.25, 30, 33; M12), das an der Seitenwand des Segments entspringt und ebenfalls an den ventralen Spangen inseriert. Die beiden Muskelpaare bewirken das Aufrichten bzw. Absenken des Penis.

Für eine Bewegung der ventralen Spangen in dorso-ventraler Richtung sorgt ein Muskelpaar (Fig.33, M11), das auf der Ventralseite der Gonocoxit-Apodeme entspringt, ventrad verläuft und an den ventralen Spangen neben den beiden anderen Muskeln inseriert. Da die ventralen Spangen die lateralen Wände des Penis bilden, verringert die Kontraktion dieses Muskelpaares dessen Lumen; dies steht in direktem Zusammenhang mit der Entleerung des Endophallus.

Innerhalb des Penis befinden sich nochmals drei weitere Muskelpaare. Ein Paar (Fig.29, 32; M3) entspringt am cranialen Ende der Dorsalbrücke, verläuft parallel zum medianen Apodem ventrad und inseriert am Endophallus (Fig.32). Bei Kontraktion von M3 wird der sackförmige Endophallus craniad gezogen und sein Lumen dadurch verkleinert, so daß dieses Muskelpaar die Wirkung von M11 unterstützt.

Ein weiteres Muskelpaar (Fig.29, M9) entspringt ebenfalls an der Innenseite von Dorsalbrücke und Dorsalsklerit an der Basis des medianen Apodems; von dort aus verläuft es — quer zur Längsachse des Penis — bis zu den dorsalen Spangen und inseriert dort. Dieses Muskelpaar kann durch Kontraktion die Stellung, vor allem die Neigung, der dorsalen Spangen verändern. Ein dazu antagonistisch wirkender Muskel ist nicht zu finden; wahrscheinlich übt die ausgedehnte membranöse Dorsalseite des Penis eine antagonistische Wirkung zu M9 aus.

Auch das Ejaculator-Apodem weist eine muskulöse Verbindung mit dem Dorsalsklerit auf (Fig.30, M5). Dieser Muskel entspringt sehr breit an der medialen Kante der ventralen Spange und inseriert — immer schmaler werdend — am cranialen Ende des Ejaculator-Apodems. Kontrahiert sich dieses Muskelpaar, so wird das gesamte Apodem caudad geschoben, was eine antagonistische Wirkung auf die Muskeln M3 und M11 hat. — Der Ductus ejaculatorius ist bis zum primären Gonoporus mit Ringmuskulatur versehen.

Innere Geschlechtsorgane (Fig.68)

Die paarigen Hoden (Ho) liegen dorsal im 4. und 5. Segment dicht beieinander; die langen und sehr dünnen Vasa deferentia (Vd) gehen caudal im Bereich des 7. und 8. Segmentes in die drüsig ausgebildete Vesicula seminalis (Ve) über. In den Endabschnitt des auf die Vesicula folgenden Ductus ejaculatorius (De) mündet ein Paar akzessorischer Drüsen (aD).

Spermatransfer

Zum Spermatransfer bei *P. ornaticornis* und *P. amplipennis* liegen keine direkten Beobachtungen vor. Es ist aber möglich, aus der Größe der sekundären Geschlechtsöffnung indirekt den Schluß zu ziehen, daß bei diesen Arten Spermatophoren eine Rolle bei der Übertragung spielen. Direkt gestützt wird diese Annahme durch die Tatsache, daß bei einer anderen Art, *P. nearctica*, die Bildung von Spermatophoren nachgewiesen ist (Leppla et.al. 1975).

3. *Dilophus febrilis* (Linnaeus, 1758)

Exoskelett

Die 8 praegenitalen Segmente sind mit ihren Terga und Sterna vollständig ausgebildet, der Terminalkomplex wird nicht invertiert getragen (Fig.34). Es sind acht Paar abdomi-

naler Stigmen vorhanden, von denen sieben in der Pleuralmembran der Segmente I—VII lokalisiert sind.

Das große Tergum IX ist als Epandrium ausgebildet, es bedeckt sowohl die Basis als auch einen großen Teil der Dorsalfläche der Gonocoxite (Fig.35). Es ist überwiegend stark sklerotisiert, nur der craniale Bereich ist weichhäutig. In dieser Zone liegen die Stigmen des 8. abdominalen Segmentes (Fig.35, 38, 39, 47; St). Sowohl in ihrer Lage als auch in ihrer Ausprägung unterscheiden sie sich sehr von den übrigen Stigmenpaaren des Abdomens. Im Vergleich zu diesen sind die Stigmen des 8. Segmentes dorsocaudad verschoben, so daß sie auf der Dorsalseite des 9. Segmentes liegen. Ihre Öffnung befindet sich auf einer auffälligen Erhebung — einer Ausstülpung der dort kaum sklerotisierten Cuticula — und ist von einem Kranz dicht stehender Reusenhaare umstellt. Dagegen liegen die abdominalen Stigmen I—VII eher etwas eingesenkt in der Pleuralmembran der Segmente und sind auch nicht von Borsten umgeben.

Das Tergum IX liegt den Gonocoxiten fest auf, da die verbindende Membran nur als schmaler Saum ausgebildet ist.

Der weichhäutige Analkegel, bestehend aus den langgestreckten Cerci (C) und dem Hypoproct (Hp), liegt meist unter dem Epandrium verborgen. Auch am expandierten Analkegel (Fig.39) ist kein sklerotisierter Bereich zu erkennen, der dem Tergum X entsprechen könnte.

Die Gonocoxite bilden ventral eine geschlossene Fläche (Fig.36; B) aus, die sich bis zur Gelenkung der Gonostyli (Gs) erstreckt. Als Ventralfläche des Segments ist sie nahezu vollständig sklerotisiert, median erstreckt sich aber vom cranialen bis zum caudalen Rand eine unpaare, weichhäutige Zone (m).

Das Gelenk zwischen Gonocoxit und Gonostylus (Gs) ist nicht eindeutig dicondyl ausgebildet (Fig.40), lediglich ventraler Gelenkhöcker (Gonocoxit) und die dazugehörige Pfanne (Gonostylus) sind vorhanden.

Der Gonostylus erscheint im Querschnitt abgeflacht; sein apikaler Rand ist gleichmäßig zu einer sehr flachen, scharfrandigen Kante ausgezogen, die keinerlei Zahnbildungen aufweist.

Der Innenraum des Genitalsegments wird ventral und lateral von den Gonocoxiten begrenzt. Auf der Dorsalseite laufen diese jederseits in das schmale Gonocoxit-Apodem aus (Fig.41; GA). Der craniale Rand der Ventralfäche ist in seinem Verlauf verhältnismäßig kompliziert aufgefaltet und bildet dort Ansatzstellen für Muskulatur aus.

Penis
Der unpaare, stark abgeflachte Penis ist zwischen den beiden Gonocoxit-Apodemen eingehängt und fest mit diesen verwachsen (Fig.41). Das median tief eingesenkte Dorsalsklerit (Ds) bildet als große, einheitliche Platte den dorsalen Abschluß des Penis, ventral wird dieser von dem ebenfalls abgeflachten Ejaculator-Apodem (E) gebildet. Die Ventralseite des Dorsalsklerits (Fig.44) zeichnet sich durch die Bildung eines langgestreckten lateralen Leisten-Paares (ventrale Leiste, vL) und einer unpaaren Platte (Endophallus-Platte, EpPl) aus. Diese median liegende Platte ist sehr stark sklerotisiert, läuft aber craniad in einer weichhäutigeren Lamelle (dL) aus. Zwischen der Oberseite des Dorsalsklerits und der Endophallus-Platte ist ein schmaler Hohlraum eingeschlossen. Sowohl die Platte als auch die dorsale Lamelle bilden den dorsalen Abschluß eines Hohlraums, des Endophallus (Fig.46b-f, Ep). Cranial biegt die dorsale Lamelle caudad

um, verläuft als ventrale Lamelle (vL) direkt über dem Ejaculator-Apodem und ist apikal mit diesem verbunden. Der Ductus ejaculatorius mündet (De) durch die ventrale Lamelle in den Endophallus, so daß der primäre Gonoporus (Fig.46d; pG) deutlich erkennbar ist. Der Endophallus ist nicht ausstülpbar. In diesen Abschnitt des Penis münden neben dem Ductus ejaculatorius auch ein Paar akzessorischer Drüsen (Fig.46b; aD). Der Endophallus öffnet sich als sekundärer Gonoporus (Fig.46, 48; Phallotrema, Pt) zwischen Dorsalsklerit und Ejaculator-Apodem. In dieser Region sind die Haare als mehrspitzige Schuppen ausgebildet, die auch das Lumen des Endophallus auskleiden (Fig.49, 50).

Muskulatur

Der Gonostylus-Adduktor (Fig.42; M1) ist kräftig ausgebildet, entspringt aber nicht direkt am cranialen Rand der Ventralwand, sondern weiter caudal und reicht in seinem Ansatz nicht bis zur Mitte der Ventralfläche; seine Insertionsstelle befindet sich an einer stark sklerotisierten Leiste der Medialfläche des Gonostylus.

Der Gonostylus-Abduktor (M2) ist nur sehr schmal ausgebildet, entspringt dorso-lateral im Genitalsegment und inseriert an der Basis des Stylus.

Das schmale Gonocoxit-Apodem ist Ansatzstelle für drei weitere Muskelpaare. Das erste (M7) erstreckt sich breit zwischen dem dorsalen Rand des Gonocoxit und dem Apodem. Die beiden anderen Muskelpaare entspringen dicht nebeneinander an den Gonocoxit-Apodemen, verlaufen ventral vom Dorsalsklerit und divergieren dort. Ein Muskel (M3) zieht mediad zum Endophallus und inseriert dort auf breiter Fläche. Seine Funktion liegt in der Verringerung des Endophallus-Volumens während der Kopulation. Das andere Muskelpaar (M11) inseriert dagegen an der ventralen Leiste (vLe) des Dorsalsklerits, es wirkt antagonistisch zu einem langen und breiten Muskel, der an der ventralen Leiste seinen Ursprung hat. Dieses langgestreckte Apodem ist desweiteren auch noch die Ansatzstelle für eine Muskelverbindung von Penis und Gonocoxit (Fig.42, 45; M4). Dieser Muskel ist distal zweigeteilt, wobei aber beide Portionen (M4a, M4b) direkt am Gonocoxit inserieren. Bei Kontraktion dieser Muskeln wird der Penis caudad geschoben und aufgerichtet.

Das einzige Muskelpaar, das ausschließlich Teile des Penis beweglich miteinander verbindet (Fig.42, 45; M5), entspringt am Ejaculator-Apodem und inseriert an der ventralen Leiste des Dorsalsklerits.

Medial wird die Ventralfläche von einem unpaaren Muskel (Fig.37, M8) überzogen, der sich über die gesamte Länge der desklerotisierten Schwächezone erstreckt. Im größten Teil seines Verlaufs ist dieser Muskel nur sehr flach, aber an seinem caudalen Ende wird er auffallend kräftiger und dicker. Zusammen mit der Schwächezone sorgt dieser Muskel für eine gewisse Beweglichkeit innerhalb der Ventralfläche, die durch Kontraktion des Muskels dachfirstartig geknickt wird; diese Knickung der Außenwand ist immer bei Tieren, die während der Kopulation fixiert worden sind, zu finden. — Der Ductus ejaculatorius ist bis zum primären Gonoporus mit einer dicken Muskularis aus Ringfasern versehen.

Innere Geschlechtsorgane (Fig.71)

Alle Organe dieses Systems sind im 8. und 9. abdominalen Segment lokalisiert. Die Vasa deferentia (Vd) sind stark verkürzt, verdickt und miteinander verschmolzen. Die

paarigen Hoden (Ho) überdecken teilweise die drüsige Vesicula seminalis (Ve). Diese erstreckt sich innerhalb des Genitalsegments bis zum cranialen Rand des Dorsalsklerits und geht erst dort in den dadurch sehr kurzen, unpaaren Ductus ejaculatorius über. Auch die in den Endophallus mündenden akzessorischen Drüsen (aD) werden zum Teil vom Dorsalsklerit überdeckt.

Spermatransfer

Wie bei *Penthetria funebris* kann auch für *D. febrilis* als sicher gelten, daß die Männchen Spermatophoren bilden. Das große Phallotrema und die besondere Differenzierung der Behaarung dieser Region stehen direkt in funktionellem Zusammenhang mit diesem Modus der Spermaübertragung. Wie bei den anderen Bibionidae muß hier aber auch offen bleiben, ob die Penis-Muskulatur ausschließlich dem Transport der Spermatophore bis in die weibliche Genitalkammer dient oder ob das Männchen mit Hilfe dieser Muskeln in der Lage ist, Sperma aus der Spermatophore zu pressen.

4. *Bibio marci* (Linnaeus, 1758), *B. leucopterus* (Meigen, 1804)

Exoskelett

Wie bei den bereits beschriebenen Vertretern der Bibionidae ist das Exoskelett der 8 praegenitalen Segmente vollständig ausgebildet, die Terminalia werden nicht invertiert getragen (Fig.51). Neben den in der Pleuralmembran der Segmente I—VII liegenden Stigmen ist noch ein weiteres, 8. Paar vorhanden.

Das am caudalen Rand etwas eingebuchtete Tergum IX (Fig.52, T IX) bildet als Epandrium den dorsalen Abschluß der Genitalkammer. Die verbindende Membran ist äußerst schmal, cranial ist das Tergum sogar mit den Gonocoxiten verwachsen.

In der Intersegmental-Membran zwischen 8. und 9. Segment ist das letzte Stigmenpaar (St VIII) des Abdomens lokalisiert. Wie bei *D. febrilis* handelt es sich hier um das dorso-caudad verschobene Stigmenpaar des 8. abdominalen Segmentes. Die Öffnung befindet sich auf einer Ausstülpung der Cuticula und ist dicht mit Haaren umstellt (Fig.62, 63).

Der Analkegel liegt meist vollständig unter dem Tergum IX verborgen. Im expandierten Zustand (Fig.54) ist zu erkennen, daß zwischen Epandrium und den langgestreckten Cerci ein weiteres, annähernd dreieckig geformtes Sklerit liegt, das Tergum des 10. Segmentes (T X). Auch der Hypoproct ist als Sklerit deutlich ausgebildet.

Das Sternum IX ist nicht nachzuweisen, die Gonocoxite bilden ventral eine geschlossene Fläche aus (Fig.53, B). Am caudalen Rand ist diese Fläche median etwas eingebuchtet, eine Erscheinung, die bei *B. leucopterus* (Fig.55) viel stärker ausgeprägt ist als bei *B. marci*. Caudal von dieser Einbuchtung sind die Gonocoxite wieder paarig, bilden also eigene Medialflächen aus. Der Boden des Genitalsegments ist stark sklerotisiert, aber medial befindet sich eine membranöse Zone (m); diese ist in ihrer Ausdehnung bei *B. marci* lediglich auf den caudalen Randbereich beschränkt, erstreckt sich aber bei *B. leucopterus* (Fig.55) als schmale Zone vom cranialen bis zum caudalen Rand der Ventralfläche.

Das Gelenk zwischen Gonocoxit und Gonostylus (Fig.56, Gs) ist dicondyl, beide Gelenkhöcker werden vom Coxit gebildet.

Die Gonostyli erscheinen im Vergleich zur Ausdehnung der Coxite eher klein; sie sind langgestreckt, schmal, verjüngen sich apikal und sind hakenförmig nach innen gebogen.

Die Gonocoxite bilden auch dorso-lateral die Außenwand des Genitalsegments. Die Gonocoxit-Apodeme (Fig.57, GA) sind langgestreckt und erreichen fast den cranialen Rand des Segments. Zwischen ihnen ist der Penis eingehängt; die diese Elemente verbindende Cuticula ist im Gegensatz zu anderen Bibionidae deutlich pigmentiert (m).

Penis

Das abgeflachte Dorsalsklerit (Fig.57, Ds) ist fest zwischen den Gonocoxit-Apodemen in der Genitalkammer eingefügt. Der craniale Rand des Sklerits ist lateral beiderseits zu einem ventrad gerichteten und bogig caudad verlaufenden Apodem ausgezogen (Fig.59; craniales Apodem, crA). An die Seitenwände des Dorsalsklerits schließen sich — ebenfalls in einem Bogen caudad verlaufende — apikal zugespitzte Spangen, die Parameren (Pa), an. Zwischen dem dorsalen Rand dieser Spangen und der lateralen Kante des Dorsalsklerits ist eine schwach sklerotisierte, sehr flexible Lamelle (Parameren-Lamelle, PaL) ausgespannt.

Auf der Ventralseite des Penis befindet sich das Ejaculator-Apodem (E); es ist hohl, und der Ductus ejuculatorius (De) liegt ihm dicht auf (Fig.61b-g). Caudal von der Einmündung des Ductus ejaculatorius in den Endabschnitt des Genitalsystems, den Endophallus (Ep), ist das Apodem als dorsal offene Halbröhre ausgebildet, in die die ventrale Portion des Ductus abgesenkt ist. Die ventrale Lamelle des Endophallus bildet hier zugleich den dorsalen Abschluß des Ejaculator-Apodems, so daß wie bei den bereits besprochenen anderen Bibionidae eine enge Verbindung zwischen ventraler Wand des Endophallus und Apex des Ejaculator-Apodems besteht. Die dorsale Lamelle des Endophallus hat einen etwas komplizierteren Verlauf als ihr ventrales Gegenstück. Sie umhüllt nämlich das caudale Ende des Ejaculator-Apodems vollständig (Fig.61c), gewinnt weiter caudad Anschluß an die Membran, die die Parameren einhüllt (Fig.61f) und diese mit dem Dorsalsklerit verbindet. Am caudalen Rand des Dorsalsklerits steht die dorsale Lamelle nur noch mit diesem in Verbindung (Fig.61g); dort öffnet sich der Endophallus in einem großen, unpaaren Phallotrema (Fig.64, 65; Pt).

Der Endophallus ist mit schuppenartig abgeflachten, mehrspitzigen Haaren ausgekleidet, wobei die Spitzen ausschließlich in Richtung des Phallotrema ausgerichtet sind (Fig.66, 67).

Muskulatur

Wie bei den bereits beschriebenen Vertretern der Bibionidae entspringt der Gonostylus-Adduktor (Fig.58, M1) ventral am Boden des Genitalsegments und inseriert an der Medialfläche des Stylus.

Der schmaler ausgebildete Abduktor (M2) entspringt latero-dorsal an der Innenwand der Gonocoxite; er inseriert außen an der Gonostylus-Basis.

Ventral erstreckt sich am caudalen Rand der Ventralfläche ein unpaarer, leicht bogig verlaufender Muskel (M8), der genau über der weichhäutigen Zone liegt. Medialer Rand der Gonocoxite und die dazugehörigen Apodeme sind ebenfalls über einen Muskel (M7) miteinander verbunden.

Die folgenden zwei Muskelpaare verbinden Elemente des Penis mit dem Exoskelett. Das erste (M4) entspringt am dorso-lateralen Rand der Gonocoxite, verläuft medio-ventrad

und inseriert am cranialen Apodem des Dorsalsklerits. Wie bei den bereits beschriebenen Vertretern der Bibionidae wird bei Kontraktion dieses Muskels der Penis caudad geschoben und gleichzeitig aufgerichtet. Ein dazu antagonistisch arbeitender Muskel ist bei den untersuchten *Bibio*-Arten nicht vorhanden.

An den Gonocoxit-Apodemen entspringt ein ebenfalls medio-caudad verlaufendes Muskelpaar (Fig.60, M3), das lateral am Endophallus inseriert. Damit ist dieses Muskelpaar durch die Veränderung des Endophallus-Volumens am Transport seines Inhalts beteiligt.

Innerhalb des Penis verlaufen zwei weitere Muskelpaare, von denen das eine sich vom cranialen Ende des Ejaculator-Apodems bis zum cranialen Apodem des Dorsalsklerits erstreckt (Fig.60, M5). Dieses Muskelpaar arbeitet als Ejaculator-Apodem-Protraktor.

Der andere, sehr breite Muskel (Fig.60, M9) ist innerhalb der bogigen Paramerenspange ausgespannt. Bei seiner Kontraktion werden die Parameren caudad geschoben; antagonistisch zu diesem Muskelpaar dürfte die flexible Parameren-Lamelle und die Eigenelastizität der gekrümmten Skleritspange selbst wirken. — Der Ductus ejaculatorius ist bis zum Endophallus mit einer Muskularis (Ringfasern) ausgestattet.

Innere Geschlechtsorgane (Fig.72)

Die langgestreckten rundlichen Hoden (Ho) haben ihren Anfang im 8. abdominalen Segment, verlaufen ein Stück craniad und biegen dann ventrad um. Die paarigen Vasa deferentia (Vd) verlaufen wieder caudad und erweitern sich zur großen Vesicula seminalis (Ve), die auf ihrer Dorsalseite teilweise von den Hoden überlagert wird. An die Vesicula seminalis schließt sich der unpaare Ductus ejaculatorius (De) an. In den Endophallus mündet ein Paar akzessorischer Drüsen (aDI), die dorsal vom Ductus liegen. Ventral befindet sich ein weiteres, großes Paar abgeflachter Drüsen (aDII), die vermutlich ebenfalls in den Ductus ejaculatorius münden.

Die Einmündung dieses Drüsenpaares konnte nicht genau lokalisiert werden, da es bei allen zur Verfügung stehenden Tieren durch die Fixierung geplatzt und artifiziell verändert gewesen ist.

Spermatransfer

Das große Phallotrema und die Auskleidung des Endophallus mit schuppenartigen Haaren, deren Spitzen ausschließlich caudad gerichtet sind, erlauben den indirekten Schluß, daß auch diese Vertreter der Bibionidae Sperma mittels einer Spermatophore übertragen. Transport und Auspressen der Geschlechtsprodukte erfolgt auch hier über eine Veränderung des Endophallus-Volumens durch das Ejaculator-Apodem und die Muskeln M3 und M5.

Mycetophiliformia

1. Cecidomyiidae: *Campylomyza flavipes* Meigen, 1818

Exoskelett

Das Abdomen dieser sehr kleinen Art (Flügellänge 1,2 mm) ist weichhäutig und zeichnet sich dadurch aus, daß die Terga nicht vollständig sklerotisiert sind (Fig.73). Das Tergum des 8. Segmentes ist lediglich als schmale Spange ausgebildet. Die letzten abdomi-

nalen Segmente werden dorsad gebogen getragen, die Terminalia sind nicht invertiert. Es sind nur vier Paar abdominaler Stigmen vorhanden, die in der Pleuralmembran der Segmente II—V liegen.

Das große, ebenfalls weichhäutige Tergum IX (Fig.74, TIX) ist nur in seinem caudalen Bereich stärker sklerotisiert und beborstet. Der Analkegel liegt vollständig unter dem Epandrium verborgen und ist gänzlich membranös.

Die Gonocoxite (G) gehen auf der Ventralseite (Fig.75) nahtlos ineinander über und bilden den Boden des Genitalsegments (B). Medial befindet sich am caudalen Rand der Ventralfläche eine ausgedehnte, kaum sklerotisierte Zone (m). Der ventrale Teil des Penis ragt ein Stück über den Rand der Genitalkammer hinaus, so daß er von außen sichtbar ist.

Die sehr großen, gleichmäßig gerundeten und beborsteten Gonostyli (Gs) sind ohne besonders differenzierte Gelenkung mit den Gonocoxiten verbunden.

Die Gonocoxite bilden auch die dorso-laterale Wandung des Genitalsegments aus (Fig.76, G). Vom medialen Innenrand der Coxite gliedern sich die Gonocoxit-Apodeme (GA) ab; diese ragen craniad weit bis in das 8. abdominale Segment hinein, konvergieren dabei etwas und vereinigen sich dann in einem völlig geschlossenen Bogen (Jugum der Gonocoxit-Apodeme, JGA).

Penis
Bei *C. flavipes* besteht der Penis aus einem Dorsalsklerit (Fig.76, Ds), dem ventral liegenden Ejaculator-Apodem (E) und einem zwischen beiden gelegenen Endophallus (Fig.80b-d, Ep).

Cranialer und lateraler Rand des Dorsalsklerits sind nahezu senkrecht ventrad gebogen und bilden so die kräftig sklerotisierten Seitenwände des Penis aus. Die über den cranialen Rand hinausragenden, langgestreckten Fortsätze (craniale Apodeme, crA, Fig.78) verbinden das Dorsalsklerit mit den Gonocoxit-Apodemen und dienen darüberhinaus als Ansatzstellen für Muskulatur.

Auf seiner Oberseite bildet das Dorsalsklerit paarige, plattenartige Ausstülpungen aus, die im caudalen Bereich apodemartig in das Innere des Penis ragen und dort Ansatzstellen für den Endophallus (Fig.80d, Ep) bilden. Der Endophallus durchzieht als von einer schwach sklerotisierten Lamelle umgebener Hohlraum den Penis. Innerhalb des Penis befindet sich auch ein Paar akzessorischer Drüsen (Fig.80b, aD), die in den Endophallus einmünden.

Weiter caudal mündet der Ductus ejaculatorius (Fig.80c, De) in den Endophallus; der Übergang des Ductus in den Endophallus ist durch den primären Gonoporus (pG) gekennzeichnet. Die Endophallus-Lamelle ist am Dorsalsklerit befestigt und öffnet sich weiter caudal in der sekundären Geschlechtsöffnung, dem Phallotrema (Fig.80e, Pt).

Das Ejaculator-Apodem (Fig.78, 79; E) ist in seinem basalen Abschnitt als stark sklerotisierter, im Querschnitt rundlicher Hohlkörper ausgebildet. An diesen langgestreckten Teil schließt sich eine auffallend große, apikale Differenzierung (aE) an, deren Oberfläche überwiegend membranös ist. Diese löffelartige Struktur ist auf ihrer Dorsalseite median tief eingesenkt, ventral befindet sich ein paariges Stützsklerit (Sk).

Lateral sind die cranialen Ränder dieser löffelartigen Differenzierung mit dem Dorsalsklerit verwachsen. Da das Ejaculator-Apodem caudad das Dorsalsklerit überragt, ist das Phallotrema nicht apikal, sondern auf der Dorsalseite des Penis lokalisiert.

Muskulatur

Die Gonostyli werden von zwei Paar Muskeln bewegt; der Adduktor (Fig.77; M1) entspringt ventral am cranialen Rand der sklerotisierten Ventralfläche, verläuft immer schmaler werdend caudad und inseriert an der Medialfläche des Stylus.

Der schmalere Abduktor (M2) entspringt dorso-lateral an der Außenwand und inseriert außen an der Basis des Gonostylus.

An der dorsalen Wand der Gonocoxite entspringt caudal ein weiteres Muskelpaar (M4), das craniad verläuft und an den cranialen Apodemen des Dorsalsklerits inseriert. Dieser Muskel richtet bei seiner Kontraktion den gesamten Penis auf.

Antagonistisch zu dieser Bewegung arbeitet ein Muskelpaar (M11), das ebenfalls an den cranialen Apodemen des Dorsalsklerits inseriert, aber weiter craniad verläuft und seinen Ursprung am Jugum der Gonocoxit-Apodeme hat.

Weiter medial entspringt am Jugum der Gonocoxit-Apodeme ein Paar sehr schmaler Muskeln (M3), die bis in den Penis ziehen und dort am Endophallus inserieren. Wie bei den bereits beschriebenen Arten ist die Hauptfunktion dieses Muskels im Spermatransfer zu sehen, da bei seiner Kontraktion das Lumen des Endophallus verkleinert wird und in ihm befindliches Material caudad aus der Geschlechtsöffnung befördert werden kann.

Das einzige Muskelpaar, das nur Teile des Penis miteinander verbindet, erstreckt sich breit auf der Ventralseite zwischen Ejaculator-Apodem und den ventralen Rändern des Dorsalsklerits (Fig.79; M5). Es arbeitet als Ejaculator-Apodem-Protraktor.

Innere Geschlechtsorgane (Fig.105)

Die langgestreckten, schlauchförmigen Hoden (Ho) verlaufen vom 5. abdominalen Segment caudad bis in das 8. Segment. Die Vasa deferentia (Vd) biegen ventro-craniad um, konvergieren stark und münden dann, unmittelbar nebeneinander liegend, in die große Vesicula seminalis (Vs). Der unpaare Ductus ejaculatorius (De), der sich caudal an die Vesicula anschließt, ist bis zu seinem Eintritt in den Endophallus mit Ringmuskulatur ausgestattet.

Spermatransfer

Direkte Beobachtungen zur Spermaübertragung liegen nicht vor, und die morphologischen Befunde lassen nicht eindeutig auf einen bestimmten Modus des Transfers — freies Sperma oder Spermatophore — schließen. Die Anordnung der Muskulatur läßt darauf schließen, daß der Mechanismus, mit dessen Hilfe die — wie auch immer gearteten — Geschlechtsprodukte aus dem Penis gepreßt werden, derselbe wie bei den Bibionidae ist.

2. Sciaridae: *Bradysia amoena* (Winnertz, 1867), *Trichosia trochanterata* (Zetterstedt, 1851)

Exoskelett

Das 8. Segment des Abdomens zeichnet sich durch ein schmales Tergum und Sternum aus, die beide über eine kurze Pleuralmembran miteinander verbunden sind. Der Terminalkomplex wird fakultativ und reversibel invertiert getragen (Fig.81), wobei das 8. Seg-

ment mitgedreht wird. Die fünf Paar abdominaler Stigmen sind in der Pleuralmembran der Segmente III—VII lokalisiert.

Das Tergum des 9. Segmentes (Epandrium) ist verhältnismäßig klein (Fig.82, T IX) und bedeckt nicht die Gonocoxite, mit denen es über eine ausgedehnte Membran verbunden ist.

An das Epandrium schließt sich der weichhäutige Analkomplex mit den Cerci (C) und dem Hypoproct (Hp) an. Deutlich als Sklerite differenzierte Bereiche sind nicht vorhanden.

Die Ventralseite des Terminalkomplexes (Fig.83) läßt kein distinktes Sternum IX erkennen. Die Gonocoxite sind hier miteinander verschmolzen und bilden so einen Teil der Ventralfläche. Medial ist diese Fläche nur sehr schwach sklerotisiert und geht weiter caudal in die Conjunctiva (Co) über, die die Verbindung zwischen Genitalkammer-Boden und Penis herstellt. Von dieser Stelle an sind die Gonocoxite bis zur Gelenkung der Styli wieder paarig und weisen eigene Medialflächen auf.

Ein deutliches Gelenk zwischen Gonocoxit und Gonostylus ist nicht vorhanden. Die Styli sind als längliche, im Querschnitt rundliche, kräftige Zangen ausgebildet, die apikal und subapikal mit kräftigen Stacheln besetzt sind (Gs).

Nach Entfernen des Epandrium und des Analkomplexes zeigt sich, daß die Gonocoxit-Apodeme (Fig.84, 85, GA) ausgesprochen kräftig entwickelt sind und craniad weit in den Innenraum hineinragen. Sie sind über eine dorsale Brücke (Db) miteinander verbunden; diese Brücke ist bei *B. amoena* vollständig membranös, bei *T. trochanterata* aber z.T. sklerotisiert.

Penis

Das Dorsalsklerit (Ds) des Penis ist fest mit der Dorsalbrücke verwachsen. Da die Dorsalbrücke in diesem Bereich aber nur sehr schwach sklerotisiert ist, kann das Dorsalsklerit — und damit der gesamte Penis — gegen die Brücke bewegt werden. Die Ränder des Dorsalsklerits sind ventrad weit ausgezogen und bilden stark sklerotisierte Seitenwände (Fig.87, 89, 93e-h) sowie die cranialen Apodeme (crA) aus.

Auf der Ventralseite des Penis befindet sich als langgestreckter, dünner, im Querschnitt rundlicher Stab das Ejaculator-Apodem (Fig.88, 93c-i; E). Caudad erweitert es sich zu einer gerundeten Skleritplatte, die auf ihrer Ventralseite mit Dörnchen besetzt ist (Dörnchenplatte, Dö; Fig.88, 93f-i, 92, 95, 96). Die Dörnchenplatte ist gegen den basalen, stabförmigen Teil des Ejaculator-Apodems beweglich und kann annähernd bis zu 90° dorsad abgebogen werden. Dörnchenplatte und Dorsalsklerit überragen caudal die Genitalkammer, während das basale Stück des Ejaculator-Apodems innerhalb der Genitalkammer liegt.

Dorsalsklerit und Dörnchenplatte sind über eine Membran (ventrale Membran, vM; Fig.88, 93f-h) miteinander verbunden, so daß ein rundum geschlossener Hohlraum entsteht, in dem der Endabschnitt des Ductus ejaculatorius verläuft. Ein deutlich abgesetzter Endophallus ist nicht vorhanden, die Intima des Endabschnittes des Ductus ejaculatorius (D. e. distalis, Ded; Fig.90) geht kontinuierlich dorsal in das Dorsalsklerit und ventral in die Dörnchenplatte des Ejaculator-Apodems über. Der Ductus ejaculatorius distalis öffnet sich in der sekundären Geschlechtsöffnung, dem Phallotrema, zwischen Dörnchenplatte und Dorsalsklerit (Fig.93h-i, 97, Pt).

Muskulatur

Der Gonostylus-Adduktor (Fig.86, M1) setzt breit am cranialen Rand der Ventralfläche an; während seines Verlaufs zweigen caudal einige Fasern als Nebenmuskeln zur Seitenwand ab. Der Adduktor inseriert mittels einer Sehne an der Medialfläche des Gonostylus.

Sein Antagonist, der Gonostylus-Abduktor (M2) entspringt latero-dorsal an der Außenwand und inseriert außen an einem kräftig ausgebildeten Höcker der Gonostylus-Basis.

Die Gonocoxit-Apodeme geben den Ursprung für weitere Muskeln. Beiderseits am dorsalen Innenrand der Gonocoxite entspringt auf breiter Fläche ein Muskel, der an den Lateralkanten der Apodeme inseriert (M7). Unpaar ausgebildet ist dagegen der Muskel, der zwischen den beiden Gonocoxit-Apodemen ausgespannt ist (M10). Es ist denkbar, daß beide Muskeln antagonistisch zueinander wirken und der Stabilisierung des Genitalsegments dienen.

Die Muskulatur des Penis setzt sich aus insgesamt fünf Paar Muskeln zusammen. Die cranialen Apodeme des Dorsalsklerits sind Insertionsstelle zweier Muskelpaare, die antagonistisch zueinander wirken. Ein Paar verläuft caudal, wo es an den Medialwänden der Gonocoxite entspringt (Fig.86, M4); das andere Paar zieht in entgegengesetzter Richtung craniad und hat seinen Ursprung am Boden des Segments (M12). Der Muskel M4 zieht den Penis caudad und richtet ihn dabei etwas auf, während die Kontraktion des Muskels M12 ihn wieder in seine Ruhestellung bringt.

Zwischen Ejaculator-Apodem und den ventralen Rändern des Dorsalsklerits überzieht ein mächtig ausgebildeter, paariger Muskel (Fig.91, M5) einen großen Teil der Ventralfläche des Penis. Antagonistisch zu diesem Ejaculator-Apodem-Protraktor wirkt ein Muskelpaar, das an den Gonocoxit-Apodemen seinen Ursprung hat, medio-caudad zieht und am Ejaculator-Apodem inseriert (Fig.91, M3). Ebenfalls an den Gonocoxit-Apodemen inseriert der paarige Muskel M11, der dorso-lateral an der Innenseite des Dorsalsklerits inseriert (Fig.91, M11). Kontraktionen dieses Muskelpaares verändern den Querschnitt des Penis (Passung im weiblichen Genitaltrakt?). — Der Ductus ejaculatorius ist nur bis zu seinem Eintritt in den Penis mit Ringmuskulatur versehen.

Innere Geschlechtsorgane (Fig.106)

Die keulenförmig verdickten Hoden (Ho) ziehen vom Dorsum des 3. abdominalen Segmentes caudad und gehen allmählich in die Vasa deferentia (Vd) über. Diese biegen im Bereich des 7./8. Segmentes wieder craniad um und münden in die blasig aufgetriebene, drüsige Vesicula seminalis (Vs); aus dieser geht caudal der langgestreckte, unpaare Ductus ejaculatorius (De) hervor. Akzessorische Drüsen sind nicht vorhanden.

Spermatransfer

Während der gesamten Kopulationsdauer von drei bis maximal zehn Minuten sind beim Männchen deutliche Pumpbewegungen im Postabdomen zu beobachten. Sofort nach Beendigung der Kopulation sind die beiden Spermathecae der Weibchen mit Sperma gefüllt. Auch konnten in keinem Stadium der Kopulation Spermatophoren weder im männlichen noch im weiblichen Genitaltrakt nachgewiesen werden. Beide Beobachtungen führen zu dem Schluß, daß bei den Sciaridae Sperma in freier Form übertragen wird.

Das Sperma wird mit Hilfe der Muskularis des Ductus ejaculatorius bis in den Penis gepumpt; dort wird es vermutlich durch rhythmische Bewegungen des Ejaculator-Apodems (Pro- und Retraktoren M3 und M5) aus dem Phallotrema gepreßt.

3. Diadocidiidae: *Diadocidia ferruginosa* (Meigen, 1830)

Exoskelett

Die Sklerite der 8 praegenitalen Segmente sind vollständig ausgebildet, auch ist das 8. abdominale Segment nicht auffällig kleiner als die vorhergehenden. Der Terminalkomplex wird nicht invertiert getragen, die morphologische Dorsalseite weist nach oben (Fig.98). Es sind fünf Paar abdominaler Stigmen vorhanden, die in der Pleuralmembran der Segmente III—VII liegen.

Das kräftig sklerotisierte Tergum IX (Fig.99, TIX) ist groß, stark gewölbt und bedeckt cranial die Gonocoxite vollständig.

Der verhältnismäßig klein ausgebildete Analkomplex mit den Cerci und dem Hypoproct liegt immer unter dem Tergum IX verborgen und kann nicht ausgestülpt werden.

Die Gonocoxite gehen auf der Ventralseite in den vollständig sklerotisierten Boden des Genitalsegments (Fig.100, B) über. Dieser erstreckt sich aber nicht bis zur Gelenkung der Gonostyli (Gs), sondern ist medial tief eingebuchtet; daher ist, über den caudalen Rand der Genitalkammer hinausragend, der dorsale Teil des Penis, das Dorsalsklerit (Ds), zu sehen.

Die im Querschnitt rundlichen Gonostyli (Gs) verjüngen sich apikal sehr stark, sind dort klauenartig gebogen und laufen in einer abgeflachten, stark sklerotisierten Doppelspitze aus. Eine deutlich ausgebildete Gelenkung zwischen Gonostylus und Gonocoxit ist nicht vorhanden.

Dorso-medial bilden die Gonocoxite (Fig.101, G) ein Paar kräftiger Gonocoxit-Apodeme (GA) aus, die craniad den Vorderrand des Segments erreichen. Der caudad über die Genitalkammer hinausragende Teil der Gonocoxite weist eine eigene mediale Wand auf.

Penis

Der Penis ist zwischen den Gonocoxit-Apodemen eingehängt (Fig.101); da diese Verbindung zum Teil membranös ist, kann der Penis gegen die Apodeme dorso-ventral bewegt werden. Das Dorsalsklerit (Ds) von *D. ferruginosa* zeichnet sich durch eine auffallend differenzierte Sklerotisierung aus. Median befindet sich ein sehr stark sklerotisierter Streifen, der craniad immer breiter wird und in den cranialen Rand des Dorsalsklerits übergeht. Dort sind auch lateral die paarigen, ventrad gekrümmten cranialen Apodeme (crA) ausgebildet. Lateral des medianen Streifens fällt das Dorsalsklerit steil ventrad ab; deutlich sind hierbei zwei unterschiedlich stark sklerotisierte Zonen zu erkennen. Die eine schließt sich direkt an den medianen Streifen an, die andere, viel weichhäutigere, greift im caudalen Bereich auf die Ventralseite über (Fig.103) und bildet dort lateral kissenartig gewölbte Polster (Po) aus. Zwischen beiden Polstern ist das Dorsalsklerit tief eingesenkt und beborstet; alle Borsten weisen mit ihren Spitzen caudad. Cranial von dieser Zone ist das Dorsalsklerit in voller Breite tief eingebuchtet.

Das schmale Ejaculator-Apodem (Fig.103, E) ist apikal sehr stark verbreitert. Lateral ist dieser Apex mit den Polstern des Dorsalsklerits verwachsen. Dort, auf der Ventral-

seite des Penis, zwischen Ejaculator-Apodem und Dorsalsklerit mündet das Phallotrema (Fig.103, 104; Pt). Der Ductus ejaculatorius (Fig.104, De) geht ohne deutlich abgesetzten Endophallus in die Geschlechtsöffnung über. Der Endabschnitt des Ductus (D. e. distalis) ist aber mit einer Intima ausgekleidet, die caudad direkt in das Ejaculator-Apodem (ventral) und das Dorsalsklerit (dorsal) übergeht. Im Bereich des Phallotrema ist die Intima ventral mit Börstchen besetzt (Fig.104).

Muskulatur

Die Bewegungsmuskulatur der Gonostyli ist wie bei den bereits beschriebenen Arten ausgebildet. Der Adduktor (Fig.102, M1) entspringt ventral am cranialen Rand der Außenwand, verjüngt sich caudad stark und inseriert an der Medialseite des Stylus; einige Fasern zweigen als Nebenmuskeln ab und sind an der Seitenwand befestigt.

Der Abduktor (M2) entspringt an der dorsalen Wand des Gonocoxits und inseriert außen an der Basis des Gonostylus; er bildet keine Nebenmuskeln aus. — Zwischen dem Innenrand der Gonocoxite und den Gonocoxit-Apodemen ist ein sehr kurzer Muskel (M7) ausgespannt.

Das craniale Apodem des Dorsalsklerits ist Insertionsstelle für die Muskulatur, die den gesamten Penis aufrichten und wieder absenken kann. Ein Paar dieser Muskeln (M4) entspringt an der Medialwand des distalen Abschnitts der Gonocoxite und verläuft craniad zu den Apodemen. Das andere, antagonistisch wirkende Muskelpaar (M12) entspringt lateral an der Dorsalwand des Gonocoxits und verläuft mediad bis zu den cranialen Apodemen des Dorsalsklerits.

Bewegungen des Ejaculator-Apodems werden ebenfalls von zwei Muskelpaaren unterstützt. Das eine entspringt an der Medialseite der Gonocoxit-Apodeme (M3) und inseriert an der Dorsalseite des verbreiterten Apex des Ejaculator-Apodems (Fig.102, 104, M3). Der Antagonist zu diesem Muskel erstreckt sich zwischen dem Basalstück des Ejaculator-Apodems und dem cranialen Apodem des Dorsalsklerits (Fig.102, M5). Wie bei den vorher beschriebenen Arten steht die Bewegung des Ejaculator-Apodems im Zusammenhang mit dem Transport des Inhalts von D. e. distalis oder Endophallus zur sekundären Geschlechtsöffnung.

Der Hohlraum, der sich caudal zwischen Dorsal- und Ventralfläche des Dorsalsklerits befindet, wird von zwei paarig ausgebildeten Muskeln durchzogen. Ein Muskelpaar (Fig.102, 104, M6) erstreckt sich vom cranialen Rand des Sklerits bis zu dessen stark sklerotisierter Spitze, das andere (Fig.102, M9) verläuft von dem stark sklerotisierten medianen Streifen zu den polsterartig ausgebildeten Seitenwänden des Dorsalsklerits. Die Arbeit beider Muskelpaare verändert den Querschnitt des Penis; bei Kontraktion des Muskels M6 wird er etwas verkürzt und ventrad abgebogen, bei Kontraktion von M9 dagegen wird der Penis verschmälert. — Die Wandung des Ductus ejaculatorius ist bis zum Phallotrema mit Ringmuskulatur ausgestattet.

Innere Geschlechtsorgane (Fig.107)

Die inneren Geschlechtsorgane von *D. ferruginosa* liegen stark komprimiert im Dorsum des 7. und 8. Segmentes. Die abgeflachten und verbreiterten Hoden (Ho), deren Paarigkeit nur schwer zu erkennen ist, gehen craniad in die kaum abgesetzten Vasa deferentia (Vd) über. Diese münden in die drüsige Vesicula seminalis (Vs), aus der caudad der unpaare, auffallend dicke Ductus ejaculatorius (De) hervorgeht. Hoden und Vasa defe-

rentia überlagern auf der Dorsalseite die Vesicula seminalis nahezu vollständig. Akzessorische Drüsen sind nicht vorhanden.

Spermatransfer
Direkte Beobachtungen zum Spermatransfer liegen nicht vor. Auch die Ausprägung des Penis bietet keinen Hinweis auf den Modus des Spermatransfers.

4. Mycetophilidae

4.1. Ditomyiinae

4.1.1. *Australosymmerus nebulosus* Colless, 1970

Exoskelett
Das 8. abdominale Segment ist viel kleiner als die vorhergehenden Segmente; Tergum und Sternum sind schmal spangenartig ausgebildet und über eine schmale Pleuralmembran miteinander verbunden (Fig.111; S VIII, T VIII). Der Terminalkomplex kann invertiert getragen werden, bei dem abgebildeten Exemplar (Fig.108) handelt es sich um eine 90°-Drehung. Die abdominalen Stigmen liegen in der Pleuralmembran der Segmente III—VII.

Das Tergum IX (Fig.109, T IX) ist sehr groß, stark sklerotisiert und bedeckt die Gonocoxite vollständig, cranial befindet sich eine schmale, streifenartige membranöse Zone.

Der Analbereich ist kompliziert gebaut und gehört zwei verschiedenen Funktionsbereichen an: Exkretion und Kopulation. Besonders auffallend sind die stark vergrößerten Cerci (C), die lateral direkt an das Epandrium anschließen. Zwischen diesen sklerotisierten Gebilden ragt ein membranöses, kegelförmiges Gebilde unter dem Tergum hervor, der eigentliche Analkonus (Ak), der nicht von den Cerci bedeckt wird. In der Ventralansicht (Fig.110, 112) zeigt sich, daß unter den Cerci ein Paar zangenartiger Sklerite verborgen liegt; diese akzessorischen Zangen (aZ) stehen senkrecht auf einer schmalen Platte (Basalplatte, Bpl; Fig.112), die direkt an der Basis der Cerci entspringt. Die akzessorischen Zangen sind mit Muskulatur versorgt und beweglich. Die Cuticula des Analkegels ist völlig frei von sklerotisierten Bereichen. Lateral ist er über Membranen mit der Basalplatte der akzessorischen Zangen verbunden. Der Analkegel entspringt an einer äußerst schmalen Skleritspange, die mit den ventrad umgebogenen Rändern des Tergum IX verwachsen ist. Diese Spange repräsentiert vermutlich das Tergum des 10. Segments (T X).

Die Ventralseite (Fig.110) weist am cranialen Rand einen deutlich abgesetzten Bereich auf, der das in die Ventralfläche integrierte Sternum des 9. Segmentes (S IX) repräsentiert. Caudal ist die Cuticula median nur sehr schwach sklerotisiert, diese Zone erstreckt sich bis zum caudalen Rand der Ventralfläche. An einer Stelle ist diese Schwächezone eingestülpt und bildet ein kurzes, unpaares Apodem (Ventralapodem, AV). Der caudale Rand des Segments ist medial zu zwei kurzen Zipfeln ausgezogen, die als mediale Gonocoxit-Fortsätze (mGF) bezeichnet werden.

Von ventral sind sowohl die akzessorischen Zangen (aZ), als auch die Gonostyli (Gs) zu sehen, die dorsal vollständig von den Cerci verdeckt werden.

Die Gelenkung der Gonostyli ist von außen nicht erkennbar, da sie cranio-mediad in die Genitalkammer hinein verschoben sind (Fig.113, Gs). Die Styli entspringen dorsal

an einem Fortsatz des Gonocoxit-Randes, dem lateralen Gonocoxit-Fortsatz (lGF). Dieser ist sklerotisiert und medio-caudad gerichtet; er endet in einer keulenförmigen, tief eingekerbten Erweiterung (Fig.114, lGF). Die Gonostyli sind mit der Basis dieses Fortsatzes verbunden. Sie sind langgestreckt, erweitern sich apikal kugelförmig und sind dort sehr stark sklerotisiert. Auf der Dorsalseite dieser Enderweiterung ist eine Reihe flacher, kammartig angeordneter Zähne ausgebildet (Zk).

Die Apodeme der Gonocoxite (GA) sind kurz und plattenartig ausgeprägt; sie sind nicht craniad, sondern mediad gerichtet; mit dem zwischen ihnen eingefügten Dorsalsklerit (Ds) des Penis sind sie fest verwachsen.

Penis

Der Penis setzt sich aus Dorsalsklerit, Endophallus und Ejaculator-Apodem zusammen. Das Dorsalsklerit (Fig.113; Ds) besteht aus einer annähernd dreieckig geformten Platte, an die sich lateral die stärker sklerotisierten, ventrad steil abfallenden Seitenwände anschließen; diese überragen caudad den Rand der Genitalkammer und laufen dort in einer doppelten Spitze zusammen.

Das Ejaculator-Apodem (Fig.117, E) ist breit, abgeflacht und nicht auffallend stark sklerotisiert. Caudal sind ein Paar kurzer, medialer Fortsätze ausgebildet, die sich an einen Bereich stärkerer Sklerotisierung anschließen. Der caudale Rand des Ejaculator-Apodems setzt sich als ventrale Lamelle (Fig.118, vL), die dorsal vom Apodem liegt, kontinuierlich in das Innere des Penis fort. Zwischen Ejaculator-Apodem und ventraler Lamelle verläuft der Ductus ejaculatorius (Fig.120, De), der durch die ventrale Lamelle in den Endophallus mündet; diese Einmündung markiert den primären Gonoporus (pG). Weiter caudal ist die Oberfläche der ventralen Lamelle mit schuppenartig abgeflachten, mehrspitzigen Haaren bedeckt, die caudad ausgerichtet sind. Die ventrale Lamelle biegt dorsad um, verläuft dann als dorsale Lamelle (Fig.119, 120; dL) caudad und geht in das Dorsalsklerit über. Der von den Lamellen eingeschlossene Hohlraum ist der Endophallus (Fig.119, 120, Ep). Dieser öffnet sich zwischen Dorsalsklerit und Ejaculator-Apodem in der unpaaren sekundären Geschlechtsöffnung (Phallotrema, Pt).

Zwischen Ejaculator-Apodem und Endophallus befindet sich ein Paar akzessorischer Drüsen (Fig.119, aD), die ebenfalls in den Endophallus münden.

Muskulatur

Der Gonostylus-Adduktor (Fig.114, M1) entspringt medio-ventral am cranialen Rand des Genitalsegments, verläuft caudad und inseriert am medio-basalen Höcker des Stylus.

Der Abduktor (M2) entspringt latero-dorsal an der Wand des Gonocoxits, verläuft ebenfalls caudad und inseriert am latero-basalen Höcker des Gonostylus.

Zwischen den plattenartig ausgeprägten Gonocoxit-Apodemen ist ein breiter, unpaarer Muskel (M10) ausgespannt, der bis an den cranialen Rand des Dorsalsklerits heranreicht.

Desweiteren inserieren an den Gonocoxit-Apodemen zwei Paar Muskeln, die beide craniad ziehen und am Boden des Genitalsegments entspringen (M12, M13). Dieser wird von einem weiteren Muskelpaar überzogen (Fig.116). Am Ventralapodem (AV) entspringt ein schmaler Muskelzug, der zum medialen Gonocoxit-Fortsatz (mGF) zieht und dort am caudalen Rand inseriert (M15).

Bei *A. fuscinervis* ist neben diesem Muskel noch ein weiteres Paar vorhanden, das ebenfalls am Ventralapodem entspringt (Fig.115). Bei dieser Art liegt das Apodem im Bereich des Sternum IX (S IX), caudal entspringt M15, lateral ein breiter, aber flacher Muskelzug, der an den Rändern des Sternum inseriert (M14).

Innerhalb des Penis sind zwei Paar Muskeln zu finden, die antagonistisch zueinander arbeiten. Auf der Ventralseite der Gonocoxit-Apodeme entspringt ein Muskel, der medio-caudad in das Innere des Penis zieht; dort inseriert er — ebenfalls ventral — am besonders verstärkten, caudalen Rand des Ejaculator-Apodems (Fig.117, M3). Dieses Muskelpaar wirkt als Ejaculator-Apodem-Retraktor.

Ebenfalls an der Ventralfläche des Ejaculator-Apodems inseriert breit ein Muskelpaar, welches das Apodem mit dem Dorsalsklerit verbindet. An den ventralen Rändern des Dorsalsklerits entspringt das Muskelpaar (M5) (Ejaculator-Apodem-Protraktor). Diese breit inserierenden Muskeln verbinden das Ejakulator-Apodem mit dem Dorsalsklerit. — Der Ductus ejaculatorius (Fig.118, De) ist bis zum primären Gonoporus mit einer Muskularis versehen.

Innere Geschlechtsorgane (Fig.139)

Die keulenförmig verdickten Hoden (Ho) beginnen im 5. abdominalen Segment; sie verlaufen caudad, wobei sie sich allmählich verjüngen. Die dünnen Vasa deferentia (Vd) biegen craniad um und münden in die Vesicula seminalis (Vs); die Vesicula ist unpaar, der paarige Ursprung dieser drüsigen Differenzierung ist aber deutlich erkennbar. Die Vesicula seminalis biegt wieder caudad um und erweitert sich sackförmig. Daran schließt sich der dicke, unpaare Ductus ejaculatorius (De) an.

Spermatransfer

Direkte Beobachtungen zur Spermaübertragung liegen für *Australosymmerus* generell nicht vor. Als indirekte Hinweise auf die Bildung von Spermatophoren können aber die schuppenartige Auskleidung des Endophallus, die Lage der akzessorischen Drüsen und das große Phallotrema gewertet werden.

4.1.2. *Symmerus annulatus* (Meigen, 1830)

Exoskelett

Das 8. Segment des Abdomens ist viel kürzer als die vorhergehenden prägenitalen Segmente, sowohl das Tergum als auch das Sternum sind lediglich spangenartig schmal ausgebildet, eine schmale Pleuralmembran ist zwischen beiden Skleriten vorhanden (Fig.121). Der Terminalkomplex kann reversibel gedreht getragen werden, Inversionen bis zu 90° sind zu beobachten. Die abdominalen Stigmen sind in der Pleuralmembran der Segmente III—VII lokalisiert.

Das Epandrium (Fig.122, T IX) bedeckt einen großen Teil der Genitalkammer; es ist erheblich breiter als lang und erreicht nicht den caudalen Rand der Gonocoxite. Das Tergum liegt den Gonocoxiten dicht auf, da die verbindende Membran nur sehr schmal ist.

Auffallendster Bestandteil des Analkomplexes sind die Cerci (C); sie sind extrem verlängert und überragen sogar noch die Gonostyli (Gs). Die Cerci schließen direkt an den

caudalen Rand des Tergum IX an und können nicht unter dieses zurückgezogen werden. Der übrige Teil des Analkonus ist häutig, weitere Sklerite sind nicht vorhanden.

Auf der Ventralseite des Terminalkomplexes (Fig.123) befindet sich medial ein unpaares Sklerit, das Sternum des 9. Segmentes (Hypandrium, S IX). Es ist langgestreckt, überragt caudad die Gonocoxite und ist in seinem caudalen Bereich tief eingeschnitten, die lateralen Zipfel sind dorsad abgebogen und auffallend stark sklerotisiert. Zwischen diesen Fortsätzen ist die Ventralseite des darunterliegenden Penis (Pe) zu erkennen. Eine schmale Membran verbindet das Hypandrium mit den beiden Gonocoxiten, so daß die sklerotisierte Ventralfläche dreigeteilt ist und flexibel erscheint.

Die Gonostyli (Gs) sind mindestens so lang wie die Coxite und außergewöhnlich differenziert. Der einheitlich sklerotisierte, beborstete Basalteil des Stylus geht auf der Ventralseite in einen Bereich über, der blasig aufgetrieben erscheint (Fig.123, aGs). Die Oberfläche ist hier deutlich gefeldert (Fig.144, 145), zu den Rändern des Stylus hin gehen diese Felder in langgestreckte Lamellen (Fig.143) über. Auf der Medialseite befindet sich zwischen Lamellenrand und sklerotisierter Stylus-Oberfläche eine schmale membranöse Zone (Fig.124, m).

Nach Entfernen von Tergum und Sternum IX zeigt sich, daß die Gonocoxite bis auf die dorsale Verbindung über Penis und Gonocoxit-Apodeme (Fig.125, GA) nicht miteinander verbunden, also durchgängig paarig sind. Vom medialen Rand der Gonocoxite gliedern sich die Gonocoxit-Apodeme (Fig.125, GA), die weit in den Innenraum ragen und zwischen denen der Penis eingehängt ist. Cranial sind die Gonocoxit-Apodeme mit einem scheibenförmigen, median eingesenkten Sklerit, der Dorsalbrücke (Db), verwachsen. Gonocoxit-Apodeme, Dorsalbrücke und Dorsalsklerit bilden eine funktionelle Einheit.

Penis
Das Dorsalsklerit des Penis ist auffallend groß (Fig.125, Ds) und überragt caudad die Gonocoxite; cranial schließt es sich direkt an die Dorsalbrücke (Db) an. Median ist die Cuticula des Dorsalsklerits nur sehr schwach sklerotisiert. Latero-caudal bildet sie ein Paar kurzer, in das Innere des Penis ragende Apodeme aus. Der caudale Rand des Dorsalsklerits ist medial leicht eingebuchtet, über diese Einstülpung ragt der Apex des Ejaculator-Apodems (E) hinaus.

Die Ventralseite des Penis (Fig.127) ist pantoffelartig ausgebildet. Im cranialen Bereich ist eine Naht zwischen Dorsalbrücke und Dorsalsklerit nicht erkennbar; es ist eine einheitliche Platte vorhanden. Die dorsale Einwölbung der Dorsalbrücke aber setzt sich auf der Ventralseite als eine deutliche Erhebung fort, die als Ansatzstelle für Muskulatur dient. Medio-caudal befindet sich ein kurzes, halbröhrenartig geformtes Sklerit, das über eine ausgedehnte, schwach sklerotisierte Membran (ventrale Membran, vM) mit den Rändern des Dorsalsklerits verbunden ist; bei diesem Sklerit handelt es sich um das stark verkürzte Ejaculator-Apodem (E). Ejaculator-Apodem und Membran bilden die ventrale Wandung eines Hohlraumes aus, der dorsal und caudal vom Dorsalsklerit begrenzt wird, cranial aber offen ist. In diesen Penis-Hohlraum hinein zieht der Ductus ejaculatorius (Fig.128, De), der bis zu dieser Stelle paarig ausgebildet ist. Das Epithel des Penis-Hohlraumes ist medial drüsig differenziert und bildet seinerseits einen kleineren Hohlraum (Fig.129a-c) aus, in den der Ductus ejaculatorius einmündet. Dieser Endophallus ist mit einer deutlich zweischichtigen Intima ausgekleidet, die Anschluß an das Dorsalsklerit gewinnt und ventral in das Ejaculator-Apodem übergeht. Der

Endophallus öffnet sich in der sekundären Geschlechtsöffnung, dem Phallotrema (Fig.129b, Pt); dieses wird von Dorsalsklerit und Ejaculator-Apodem umschlossen.

Muskulatur

Die Muskelausstattung des männlichen Genitale von *S. annulatus* erscheint stark reduziert, insgesamt sind in diesem Bereich nur vier Paar Muskeln vorhanden.

Der Gonostylus-Adduktor (Fig.126, M1) entspringt breit an der Ventralfläche der Gonocoxite, die Insertionsstelle befindet sich an der Medialseite der Styli.

Der weniger stark entwickelte Gonostylus-Abduktor (M2) hat seinen Ursprung an der dorsalen Innenfläche der Coxite; er inseriert lateral an einem stark sklerotisierten Höcker der Stylusbasis.

Der Penis wird von zwei Paaren longitudinal angeordneter Muskeln durchzogen. Das erste, lateral verlaufende Paar (Fig.126, 128; M11) entspringt an der medialen Innenkante der Gonocoxite; seine Insertionsstelle ist das paarige, ventrad gerichtete caudale Apodem des Dorsalsklerits. Bei Kontraktion dieses Muskelpaares wird der Penis aufgerichtet und in seine Kopulationsstellung gebracht. Das medial verlaufende Muskelpaar (Fig.126, 128; M3) hat seinen Ursprung am Dorsalsklerit im cranialen Bereich zwischen den beiden Gonocoxit-Apodemen. Diese Muskeln durchziehen den Penis in seiner ganzen Länge, wobei sie in der Nähe der Insertionsstelle völlig parallel und dicht aneinandergelegt verlaufen. Sie inserieren am cranialen, in das Innere des Penis ragenden Rand des Ejaculator-Apodems. Ein dazu direkt antagonistisch wirkender Muskel ist nicht vorhanden. Rhythmische Kontraktionen des Muskelpaares M3 befördern den Inhalt des Endophallus über das Phallotrema nach außen. — Der paarige Abschnitt des Ductus ejaculatorius ist bis zu seinem Eintritt in den Endophallus muskularisiert (Ringfasern).

Innere Geschlechtsorgane (Fig.140)

Die inneren Geschlechtsorgane von *S. annulatus* sind durchgehend paarig und schlauchförmig ausgebildet, so daß die Differenzierung in verschiedene Abschnitte von außen nur schwer zu erkennen ist. Die an ihren Enden leicht keulenförmig verdickten Hoden (Ho) liegen im Bereich der Segmente V und VI, verlaufen ein Stück caudad und biegen dann craniad um. In diesem Bereich gehen sie in die Vasa deferentia (Vd) über, die — dicht aneinandergelegt — craniad bis zum 4. abdominalen Segment verlaufen. Dort münden sie in die leicht verdickten, ebenfalls paarigen Vesiculae seminales (Vs); diese biegen wieder caudad um und ziehen bis in das 7. Segment. Dort geht aus ihnen der extrem dünne, ebenfalls paarige Ductus ejaculatorius (De) hervor. Akzessorische Drüsen sind nicht vorhanden.

Spermatransfer

Direkte Beobachtungen zum Spermatransfer liegen nicht vor. Allerdings deuten die Ausprägung des Ductus ejaculatorius (bis zum Endophallus paarig) und das verhältnismäßig kleine Phallotrema auf eine Übertragung flüssigen Spermas hin.

4.1.3. *Ditomyia fasciata* (Meigen, 1818)

Exoskelett

Das 8. Segment des Abdomens ist sehr viel schmaler als die vorhergehenden, eine Pleuralmembran ist nicht vorhanden und Tergum und Sternum sind zu einem Skleritring miteinander verschmolzen (Fig.130). Die Terminalia werden nicht invertiert getragen. Es sind nur drei Paare abdominaler Stigmen vorhanden; sie liegen in der Pleuralmembran der Segmente IV—VI.

Das Tergum IX (Fig.131, T IX) und der Analkomplex sind — verglichen mit den Ausmaßen der übrigen Teile — verhältnismäßig klein. Die direkt an das Epandrium anschliessenden Cerci (C) sind die einzigen stärker sklerotisierten Elemente des Analkomplexes.

Die Gonocoxite sind sowohl dorsal als auch ventral miteinander zu einer Genitalkapsel verschmolzen (Gkp). Das craniale Foramen dieser Kapsel (Fig.134, crF) erstreckt sich bis auf deren Dorsalseite und wird vom Epandrium verdeckt. Die Genitalkapsel verjüngt sich caudad stark; in diesem Bereich ist ein weiteres Foramen (dorso-caudales Foramen, dcF) lokalisiert, in das ein Sklerit, das Dorsalsklerit (Ds), eingehängt ist; es füllt fast das gesamte Foramen aus und überragt caudal auch noch den Rand der Genitalkapsel.

Median ragt von der Dorsalseite ein unpaares Apodem (Genitalkapsel-Apodem, GkpA; Fig.133b) in das Innere der Genitalkapsel und erstreckt sich vom cranialen bis zum dorso-caudalen Foramen. Gonocoxit-Apodeme sind nicht ausgebildet. Die Ventralseite der Kapsel (Fig.132) läßt keine Spur eines Sternum IX erkennen. Eine median liegende, wulstförmige Erhebung, die sich vom cranialen bis zum caudalen Rand der Genitalkapsel erstreckt, ist dort u-förmig tief eingebuchtet. Diese Einbuchtung wird vollständig vom Ejaculator-Apodem (E) ausgefüllt.

Die Gonostyli (Gs) sind länger als die Genitalkapsel, im Querschnitt dreieckig, und ihr Apex ist medial hakenförmig eingekrümmt. Entlang der Medialseite erstreckt sich kammartig eine Reihe stark sklerotisierter, abgeflachter Zähnchen (Zähnchenkamm, Zk; Fig.146).

Penis

Der Penis (Fig.136, 137; Pe) befindet sich ventral am caudalen Rand der Genitalkapsel. Ein Dorsalsklerit (Ds) ist zwar vorhanden und auch funktionell mit dem ventral liegenden Ejaculator-Apodem verbunden, aber die Struktur, mit deren Hilfe Sperma übertragen wird, ist allein das Ejaculator-Apodem. Demzufolge gehört das Dorsalsklerit nicht zum Penis von *D. fasciata*, wird aber wegen der engen Lagebeziehung hier mitbehandelt.

Das Dorsalsklerit ist auf seiner Oberseite median tief eingewölbt, seine lateralen und caudalen Ränder erstrecken sich weit ventrad (Fig.136, Ds). Lateral sind am cranialen Rand paarige Fortsätze, die cranialen Apodeme (crA) ausgebildet. In Frontalansicht (Fig.147, 148) ist zu erkennen, daß der ventrad lang ausgezogene, nur schwach sklerotisierte caudale Rand des Dorsalsklerits dicht behaart ist: seine Lage direkt über dem Penis legt den Schluß nahe, daß ihm eine Funktion als Sinnespolster während der Copula zukommt.

Der Penis selbst ist paarig (Fig.136, 137, 138, 148, 149; Pe). Er besteht aus zwei kleinen, sehr stark sklerotisierten, spitz zulaufenden Röhrchen, die am Ejaculator-Apodem ent-

springen. Das Apodem ist in zwei deutlich verschiedene Abschnitte differenziert. Der apikale Bereich (aE) ist als Hohlraum (Fig.138b-f) ausgebildet, der von einer sklerotisierten Cuticula umhüllt wird. Caudal gliedern sich aus diesem Hohlraum die Penes ab (Fig.138b-d). Weiter craniad gewinnt die apikale Differenzierung Anschluß an die Genitalkapsel (Fig.138f). Ein tiefer Einschnitt in der dorsalen Cuticula des Apex setzt sich als basaler Abschnitt des Ejaculator-Apodems (Fig.138g,h, E) in das Innere der Genitalkapsel fort. Dieser Teil ist röhrenförmig und stark sklerotisiert.

Ein Endophallus ist nicht vorhanden, der paarige Ductus ejaculatorius (Fig.136, De) verläuft dorsal vom Basalstück des Ejaculator-Apodems und tritt dann in die apikale Differenzierung des Apodems ein. Dort verlaufen die beiden Gänge direkt unter der Oberfläche und gehen dann direkt in die Penes über. Die Geschlechtsöffnungen — es handelt sich um primäre Gonopori — sind auf der Dorsalseite am Apex der Penes lokalisiert (Fig.149).

Muskulatur

Der fächerförmig entwickelte Gonostylus-Adduktor (Fig.135, M1) entspringt median an der ventralen Wand der Genitalkapsel; er verläuft latero-caudad und inseriert nahe der Basis des Stylus an dessen Medialfläche.

Der Gonostylus-Abduktor (Fig.134, M2) hat seinen Ursprung am Genitalkapsel-Apodem, verläuft quer zur Längsachse der Kapsel und inseriert an der Basis des Stylus.

Die übrigen Muskeln können als Bewegungsmuskulatur der Penes (und des Dorsalsklerits) zusammengefaßt werden. Am Dorsalsklerit inserieren zwei Muskelpaare. Eines entspringt am medialen Rand des dorso-caudalen Foramen, verläuft ventrad und inseriert an den lateralen Rändern des Dorsalsklerits (Fig.134, 136, M4); die Kontraktion dieses Muskels zieht das Dorsalsklerit caudad. Das andere Muskelpaar (Fig.136, M5) entspringt am Basalstück des Ejaculator-Apodems, verläuft nahezu senkrecht dorsad und inseriert im Innern des Dorsalsklerits; mit seiner Hilfe können die Penes dorso-ventral bewegt werden.

Das Ejaculator-Apodem ist über zwei weitere Muskelpaare mit der Genitalkapsel verbunden; beide entspringen an der ventralen Wand der Kapsel. Das eine inseriert an der Übergangszone zwischen Basalstück und apikaler Differenzierung des Ejaculator-Apodems und fungiert als Retraktor (Fig.136, M3). Das andere Muskelpaar (Fig.135, M16) erstreckt sich zwischen dem Basalstück und dem Rand der medianen Erhebung der Genitalkapsel; es arbeitet antagonistisch zu Muskel M3 als Protraktor.

Die Muskelpaare M3, M5 und M16 dienen der Justierung der Penes an den entsprechenden Stellen des weiblichen Genitaltraktes (Öffnungen der paarigen Spermathecae). — Der paarige Ductus ejaculatorius ist bis zu seinem Übergang in die Penes mit einer dicken Muscularis aus Ringfasern versehen.

Innere Geschlechtsorgane (Fig.141)

Die im 7. abdominalen Segment beginnenden, sehr dünnen, paarigen Hoden (Ho) gehen cranial in die dicht nebeneinander liegenden, verdickten Vasa deferentia (Vd) über. Diese münden im 3./4. Segment in die überwiegend paarigen Vesiculae seminales (Vs) ein, aus denen caudad die langgestreckten, dünnen Gänge des paarigen Ductus ejaculatorius (De) hervorgehen; diese bilden ventral von den Vesiculae eine Schleife, verlaufen direkt nebeneinanderliegend caudad durch die Genitalkapsel bis in die Penes. Akzessorische Drüsen sind nicht ausgebildet.

Spermatransfer

Die nur minutenlang dauernde Kopulation (etwa fünf bis zehn Minuten) wird von rhythmischen Pumpbewegungen im Postabdomen des Männchens begleitet. Weder bei den Weibchen noch bei den Männchen konnten im Genitaltrakt Spermatophoren aufgefunden werden. Dies und die Ausprägung der Penes lassen den Schluß zu, daß bei dieser Art das Sperma in freier Form übertragen wird. Die dicke Muskularis aus Ringfasern, die das enge Lumen des paarigen Ductus ejaculatorius umhüllt, drückt durch peristaltische Kontraktionen das Sperma bis in die Penes und aus diesen in die weiblichen Receptacula.

4.2. Keroplatinae: *Platyura marginata* Meigen, 1804[1]

Exoskelett

Das 8. abdominale Segment ist viel kürzer als die übrigen, Tergum und Sternum sind durch eine Pleuralmembran voneinander getrennt (Fig.150). Der Terminalkomplex wird nicht invertiert getragen. Die abdominalen Stigmenpaare liegen in der Pleuralmembran der Segmente I—VII.

Das Tergum IX (Fig.151, T IX) ist klein, breiter als lang und bedeckt lediglich die Basis der Gonocoxite (G), so daß zum Teil die Gonocoxit-Apodeme (GA) sichtbar sind. Die direkt anschließenden Cerci (C) und der große Hypoproct sind sklerotisiert; die langgestreckten Cerci erreichen den caudalen Rand der Genitalkammer.

Der Boden des Genitalsegments (Fig.152, B) ist bis auf eine unpaare membranöse Zone (m) am caudalen Rand durchgehend sklerotisiert, Anteile des Sternum des 9. Segmentes sind nicht erkennbar. — Die mediad gerichteten Gonostyli (Gs) sind einteilig, länger als breit und im Querschnitt abgeflacht; apikal sind sie zu zwei Spitzen ausgezogen.

Die Gonocoxite bilden die ventrale, laterale und dorso-laterale Wandung des Genitalsegments (Fig.153, G). Dorsomedial laufen sie jederseits in ein Apodem (Gonocoxit-Apodem, GA) aus, das den cranialen Rand des Segments erreicht. Zwischen diesen Gonocoxit-Apodemen ist der Penis eingehängt; die Verbindung ist durch membranöse Bereiche sehr flexibel.

Penis

Die Gestalt des Penis wird von dem ausgedehnten, caudal fast den gesamten Raum zwischen den Gonocoxiten einnehmenden Dorsalsklerit (Fig.153, Ds) dominiert. Die Cuticula des Dorsalsklerits bildet median ein ventrad nach innen gerichtetes Apodem (medianes Apodem, meA; Fig.153, 159) aus, das von außen als schmale, stark sklerotisierte Zone erkennbar ist. Caudal sind dorso-lateral zwei achselklappenartig erhabene Skleritplatten vorhanden, deren cranialer Rand gezähnt ist (Fig.155). Der caudale Rand des Dorsalsklerits geht in eine nur sehr schwach sklerotisierte, ventrad gerichtete Zone über, die von den Spitzen der Parameren (Pa) durchbrochen wird.

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[1] Von dieser Art standen nur zwei verhältnismäßig schlecht erhaltene Individuen zur Verfügung; bei beiden lagen die inneren Geschlechtsorgane in stark atrophierter Form vor, so daß zu diesem Merkmalskomplex keine Daten vorgelegt werden können.

Die Ränder des Dorsalsklerits sind lateral weit ventrad ausgezogen und greifen auch auf die Ventralseite des Penis über (Fig.156). Cranial sind ein Paar kurze Fortsätze, die cranialen Apodeme (crA), ausgebildet. Die Parameren, die als langgestreckte, geschwungene Skleritspangen den vom Dorsalsklerit gebildeten Hohlraum durchziehen, entspringen medial am ventralen Rand des Dorsalsklerits (Fig.156, Pa). Zwischen diesem und den Parameren ist keine Grenze festzustellen, beide Elemente gehen nahtlos ineinander über. Die Parameren verlaufen in einem kleinen Bogen laterad und biegen dann caudad um. Am caudalen Rand des Penis durchbrechen sie den schwach sklerotisierten Teil des Dorsalsklerits, so daß ihre Spitzen wie in einer Führungsschiene zwischen beiden Bereichen hervorragen. In der Seitenansicht (Fig.157) ist zu erkennen, daß die Parameren basal als senkrecht stehende Skleritplatte (Basalplatte, Bpl) ausgebildet sind, die sich erst weiter apikal zu schmalen Spangen verjüngen.

Das Ejaculator-Apodem (Fig.156, E) ist deutlich in zwei verschieden differenzierte Abschnitte gegliedert. Basal ist es als kurzes, stark sklerotisiertes Rohr ausgebildet, das sich apikal ankerförmig erweitert. Daran schließt sich der langgestreckte, weichhäutige apikale Teil (aE) an, der wie eine Halbröhre geformt ist.

Ein Endophallus, zwischen Dorsalsklerit und Ejaculator-Apodem gelegen, ist nicht vorhanden. Der unpaare Ductus ejaculatorius (Fig.159, De) zieht zwischen beiden Elementen in den Penis und geht dort kontinuierlich in den Ductus ejaculatorius distalis (Ded) über. Die Intima, die diesen auskleidet, erstreckt sich bis in das Dorsalsklerit (dorsale Lamelle) und schließt auch direkt an das Ejaculator-Apodem an (ventrale Lamelle). Die ventrale Lamelle ist mit Häkchen besetzt, deren Spitzen caudad gerichtet sind. Dort mündet — zwischen Dorsalsklerit und Ejaculator-Apodem — der Ductus ejaculatorius distalis in einem großen, unpaaren Phallotrema (Pt) aus.

Muskulatur

Der Gonostylus-Adduktor (Fig.154, M1) entspringt breit am cranialen Rand der Ventralfläche; er verläuft sich rasch verjüngend caudad und inseriert an der Medialfläche des Stylus.

Der Gonostylus-Abduktor (M2) ist sehr viel schmaler ausgebildet; er entspringt dorsolateral an der Innenwand der Gonocoxite und inseriert außen an einem basalen Höcker des Gonostylus.

Zwischen den Gonocoxit-Apodemen und dem medialen Rand der Coxite verläuft ein schmaler Muskelzug (M7). Zwei Paar antagonistisch arbeitender Muskeln können den gesamten Penis aufrichten und wieder absenken. Beide inserieren an den cranialen Apodemen des Dorsalsklerits. Das eine Paar verläuft caudad und entspringt an der dorsalen Wand der Gonocoxite (M4), das andere zieht in die entgegengesetzte Richtung zum cranialen Rand der Ventralfläche, wo es seinen Ursprung hat (M12).

Die Gonocoxit-Apodeme sind Ursprungsort für ein Muskelpaar, das mediad zum Penis zieht und dort an der ankerförmigen Erweiterung des Ejaculator-Apodems inseriert (Fig.155, M3). Dieser Muskel arbeitet als Retraktor des Ejaculator-Apodems. Innerhalb des Penis finden sich noch drei weitere Muskelpaare (Fig.155, 156, 158). An dem stabförmigen, basalen Abschnitt des Ejaculator-Apodems inseriert ein Muskel, der seinen Ursprung am ventralen Rand des Dorsalsklerits hat (Fig.156, M5). Dieses Muskelpaar wirkt als Ejaculator-Apodem-Protraktor antagonistisch zu M3. Beide Muskeln verändern antagonistisch das Lumen des Endabschnittes des Ductus ejaculatorius und dienen damit dem Ausleiten der Geschlechtsprodukte. Direkt unter der Dorsalfläche des

Sklerits verläuft ein Muskel, der breit am cranialen Rand entspringt und am caudalen Rand direkt an der Basis des medialen Apodems inseriert (Fig.155, M6).

Auch die Seitenwand des Dorsalsklerits wird von einem mächtig ausgebildeten Muskel (Fig.158, M9) überzogen. Er entspringt caudal direkt an der Innenseite des Dorsalsklerits, verläuft cranio-ventrad und inseriert an der Basalplatte der Parameren. Bei Kontraktion dieses Muskels werden die Parameren caudad geschoben; die Eigenelastizität der gekrümmten Spange dürfte antagonistisch zum Parameren-Muskel wirken. — Der Ductus ejaculatorius ist durchgehend mit einer Muskularis aus Ringfasern versehen.

Spermatransfer

Auf den Modus der Spermaübertragung kann nur indirekt geschlossen werden, da keine direkten Beobachtungen vorliegen. Die Größe des Phallotrema und die Beborstung des Ductus ejaculatorius distalis weisen auf die Bildung von Spermatophoren hin. Die Entleerung des Endophallus-Inhalts erfolgt — wie bei den bereits beschriebenen Arten — durch die Bewegung des Ejaculator-Apodems.

4.3. Bolitophilinae: *Bolitophila tenella* Winnertz, 1863

Exoskelett

Das langgestreckte Abdomen (Fig.160) weist hinsichtlich seiner Terga und Sterna keinerlei Besonderheiten auf, das 8. Segment ist nicht auffallend kurz. Die Terminalia werden nicht invertiert getragen. Die vier abdominalen Stigmenpaare liegen in der Pleuralmembran der Segmente IV—VII.

Das Tergum des 9. Segmentes (Fig.161, T IX) ist breiter als lang und bedeckt lediglich die Basis der Gonocoxite (G). Das Tergum X ist nicht ausgebildet. Der Analkomplex besteht aus den langen Cerci (C) und einem großen Hypoproct (Hp); alle Elemente sind sklerotisiert.

Die Ventralseite der Terminalia (Fig.162) ist als vollständig sklerotisierte, einheitliche Fläche ausgebildet (B); das Sternum IX ist als distinktes Element nicht vorhanden. Medio-caudal bildet die Ventralwand eine paarige Erhebung aus, deren Medialflächen polsterartig verdickt und dicht behaart sind. Zwischen diesen Polstern setzt sich die Ventralfläche nur schwach sklerotisiert in das Innere der Genitalkammer fort.

Eine Gelenkung zwischen Gonocoxit und Gonostylus ist nicht besonders ausdifferenziert. Die Gonostyli sind komplex gebaut (Fig.161, 162; Gs). Ihre Dorsalfläche erscheint wie ein einteiliger Stylus, der apikal dornartig ausgezogen ist; die Ventral- und die tief ausgehöhlte Medialseite aber zeichnen sich durch eine ausgedehnte partielle Desklerotisierung aus. Eingebettet in dieses membranöse Feld liegt die Basis einer langen, zugespitzten Sklerotspange, die erst mediad verläuft, dann aber caudad umbiegt (Fig.162, GsSp1). Aufgrund ihrer Verankerung in dem membranösen Feld ist diese Spange beweglich. Ein weiterer sklerotisierter Fortsatz (Fig.161, GsSp2) entspringt in der Höhlung zwischen dorsaler und ventraler Styluswand. Basal ist diese Spange sehr schmal, erweitert sich aber apikal plattenartig und läuft dort in einer Reihe dicht stehender Lamellen aus.

Nach Entfernen von Epandrium und Analkomplex (Fig.163) zeigt sich, daß das Dorsalsklerit (Ds) des Penis mit dem medialen Rand der Gonocoxite verschmolzen ist; frei

in den Innenraum ragende Gonocoxit-Apodeme sind nicht ausgebildet, aber die Dorsal-brücke (Db) ist durch eine Naht deutlich vom Dorsalsklerit abgesetzt.

Penis

Das Dorsalsklerit (Fig.165, 166; Ds) bildet median ein mächtiges, ventrad gerichtetes Apodem (medianes Apodem, meA) aus, das sich kontinuierlich vom cranialen zum caudalen Rand des Sklerits erstreckt.

Caudal sind die Seitenränder des Dorsalsklerits weit ventrad gerichtet und dort zu einem langen, spitz zulaufenden Apodempaar (caudales Apodem, caA) ausgezogen. An diesem Teil der Dorsalsklerit-Seitenwand entspringt die Basis der Parameren (Pa). Diese apikal zugespitzten Skleritspangen verlaufen erst in einem Bogen craniad und biegen dann caudad um; im Bereich dieser Biegung ist ein Fortsatz als Muskelansatz-stelle (Ma, Fig.167) ausgebildet. Die stark sklerotisierte Parameronspange ist mittels Membranen sowohl mit dem Dorsalsklerit als auch mit dem ventralen Element des Penis verbunden (Fig.170f-k).

Das mediane Apodem (meA) liegt direkt einem rundlichen Hohlkörper auf, dessen Wände partiell sehr stark sklerotisiert sind. Dieser Raum wird hier als Pumpenraum (Fig.166, 170, Pu) bezeichnet. Der Pumpenraum verjüngt sich allmählich caudad und geht dann in einen englumigen Gang, den Spermagang (Fig.170h-l, Spg) über; dieser behält dorsal den Kontakt zum Dorsalsklerit, das in diesem Bereich eine vom medialen Apodem ausgehende, stark sklerotisierte Röhre bildet (Fig.170i-j). Die Wandung des Spermaganges geht im Apex des Pumpenkomplexes in diese Röhre über; sie öffnet sich in einem paarigen Phallotrema (Fig.170l-n, 172,, Pt). Die beiden Öffnungen sind zwar groß, aber weitgehend mit einer Membran verschlossen; die eigentliche Austrittsöff-nung für das Sperma ist sehr klein (Fig.173).

Ventral schließt sich an den Pumpenraum ein weiteres Element der Spermapumpe an, das Ventralsklerit (Fig.168, 170c-j, Vsk). Cranial umgreift es halbschalenartig die Wand des Pumpenraumes; ventral davon bildet es einen kleinen Hohlraum (Pumpenvorraum, PuVo; Fig.170e,f), in den die paarigen akzessorischen Drüsen einmünden. Der Endab-schnitt der Drüsengänge ist stark sklerotisiert (Fig.170c, aD) und fest mit dem Ventral-sklerit verbunden.

Caudal von der Eintrittsstelle der Drüsen mündet der Ductus ejaculatorius in den Pum-penvorraum ein; seine sackartige Enderweiterung schließt direkt an das Ventralsklerit an. In diesem Bereich bildet das Ventralsklerit lateral ein stark sklerotisiertes, klappen-artig geformtes Skleritpaar aus, das den Ductus ejaculatorius in der Region des primä-ren Gonoporus (Fig.168; pG) umgreift. Diese Klappen sind so angeordnet, daß sie den Übergang von Sperma aus dem Ductus ejaculatorius in den Pumpenvorraum regulieren können; sie können daher als Ventilsklerite (Vesk) bezeichnet werden. Das Lumen des Pumpenvorraumes verschmälert sich caudad stark; in diesem Bereich ist der Vorraum mit dem eigentlichen Pumpenraum über einen gewebigen Strang verbunden, der ver-mutlich einen Gang (Verbindungsgang, Vbg; Fig.170f,g) umschließt. Durch diesen Gang gelangt der Inhalt des Pumpenvorraumes (Sperma und Sekret der akzessorischen Drüsen) in den Pumpenraum.

Es ist nicht möglich gewesen, diesen Gang direkt zu dokumentieren, da das sehr zarte Gewebe durch die unzulängliche Alkoholfixierung (Material aus faunistischen Auf-sammlungen!) vollständig kollabiert ist. Funktionsmorphologische Überlegungen zum

Weg des Spermas aus dem Ductus ejaculatorius zum paarigen Phallotrema führen aber zu dem Schluß, daß dieser Gang vorhanden ist.

Caudal vom Pumpenvorraum ist das Ventralsklerit nur noch als schwach sklerotisierte, fleischige Platte ausgebildet, die Anschluß an die Parameren gewinnt und sich zu einem Hohlraum mit paarigem Lumen erweitert (Fig.170h,i). Das Ventralsklerit erreicht nicht den Apex des Penis.

Muskulatur

Der Gonostylus-Adduktor (Fig.164, M1) entspringt am cranialen Rand des Genitalsegments und an der Seitenwand der Gonocoxite. Er verläuft caudad und inseriert breit medial an der Basis der Gonostyli.

Der außergewöhnlich kurze und breite Gonostylus-Abduktor (M2) entspringt dorsal an der Innenwand der Gonocoxite und inseriert lateral an der Basis der Styli.

Der Penis wird durch zwei antagonistisch wirkende Muskelpaare dorso-ventral bewegt (Vorschieben, Aufrichten und Zurückziehen, Absenken). Beide Muskeln inserieren am caudalen Apodem des Dorsalsklerits; der eine entspringt cranial an der Seitenwand der Gonocoxite (M12), der andere dorsal am caudalen Rand der Coxite (M4).

Innerhalb der Spermapumpe sind zwei weitere Muskelpaare ausgebildet. Direkt an der Basis des medianen Apodems des Dorsalsklerits entspringt ein Muskelpaar (Fig.167, 170e, M3), das ventrad verläuft und an den sklerotisierten Flächen des Pumpenraumes inseriert. Bei seiner Kontraktion wird das Apodem, das als Pumpenkolben aufgefaßt werden kann, in den Pumpenraum gedrückt, dessen elastische Wandung dadurch eingedellt wird. Diese Elastizität dürfte antagonistisch zu der Muskelkontraktion wirken. Der Parameren-Muskel (Fig.167, M9) entspringt caudal an der Innenfläche des Dorsalsklerits, verläuft cranio-ventrad und inseriert an einem Fortsatz der Paramerenspange. Bei Kontraktion dieses Muskelpaares werden die Parameren caudad geschoben. Ein antagonistisch wirkender Muskel ist nicht vorhanden; vermutlich übt die Eigenelastizität der gekrümmten Paramerenspange eine antagonistische Wirkung aus.

Zwischen den beiden Ventilskleriten der Spermapumpe ist ein unpaarer Muskel (Fig.169, M16) ausgespannt, bei dessen Kontraktion der primäre Gonoporus geöffnet wird.

Innere Geschlechtsorgane (Fig.171)

Die paarigen Hoden (Ho) liegen im Bereich der abdominalen Segmente VI und VII. Die dünnen, paarigen Vasa deferentia (Vd) verlaufen caudad und gehen dann in die verdickten, ebenfalls paarigen Vesiculae seminales (Vs) über. Diese vereinigen sich zum unpaaren Ductus ejaculatorius (De), der in das Genitalsegment zieht. Dort erweitert er sich — ventral der Spermapumpe (Sppu) — zu einem blasig aufgetriebenen Spermareservoir (Spr), das in den Vorraum des Pumpenkomplexes einmündet. Die paarige akzessorische Drüse (aD) mündet ebenfalls in den Pumpenvorraum.

Spermatransfer

Obwohl keine direkten Beobachtungen zum Spermatransfer vorliegen, lassen die Ausprägung des Dorsalsklerits und Anordnung der Muskulatur keinen Zweifel daran aufkommen, daß Sperma ohne die Bildung von Spermatophoren in freier Form übertragen wird. Das Sperma, welches in der Enderweiterung des Ductus ejaculatorius gesammelt wird (bei allen präparierten Tieren ist dieser Teil des Ductus immer mit Spermien-Bün-

deln gefüllt gewesen), wird durch die Bewegung der Ventilsklerite in den Pumpenvorraum gesaugt. Von dort muß es in den eigentlichen Pumpenraum gelangen, denn nur dieser kommuniziert mit der paarigen Geschlechtsöffnung. Wahrscheinlich nimmt das Sperma den Weg über den gewebigen Verbindungsgang, wobei es durch die Pumpbewegungen des medianen Apodems (Pumpenkolbens) angesaugt wird.

Der Inhalt des Pumpenraumes kann dann über die Geschlechtsöffnungen nach außen gepreßt werden; dabei wird vermutlich durch die starke Lumenverengung des dickwandigen Spermaganges (geringe Elastizität) und durch die winzigen Geschlechtsöffnungen ein hoher Druck entwickelt.

4.4. Mycetophilinae: *Mycetophila fungorum* (De Geer, 1776)

Exoskelett

Das praegenitale Abdomen besteht aus acht Segmenten, wobei die beiden letzten (VII und VIII) erheblich schmaler als die vorhergehenden ausgebildet sind (Fig. 174). Beim lebenden Tier sind diese Segmente teleskopartig in das 6. Segment eingezogen und von außen nicht erkennbar.

Tergum und Sternum VII sind durch eine Pleuralmembran voneinander getrennt (Fig.176). Zwischen den Sterna der Segmente VII und VIII befindet sich ein weiteres Sklerit; hierbei handelt es sich um die partiell sklerotisierte Conjunctiva beider Segmente (Fig.176, Co). Stärker abgewandelt sind die Sklerite des darauf folgenden 8. Segmentes. Das Tergum (T VIII) ist dorsal spangenartig schmal, erweitert sich aber lateral und ist dort direkt mit dem zugehörigen Sternum verwachsen (S VIII). Eine Pleuralmembran zwischen beiden Skleriten ist nicht ausgebildet. Das Sternum VIII ist caudad verlängert und unterlagert zungenförmig die Ventralseite der Terminalia (Fig.175, S VIII). Die ventrale Conjunctiva zwischen Sternum und Terminalia ist schmal und wie die vorhergehende stark sklerotisiert (Fig.176, Co). Die Terminalia werden nicht invertiert getragen.

Die Sterna der Segmente II bis VI weisen bezüglich ihrer Sklerotisierung eine Besonderheit auf: sie sind durch Bereiche differenzierten Sklerotisierungsgrades in härtere Streifen und dazwischenliegende flexiblere Felder aufgeteilt (Fig.175). Dies hat zur Folge, daß die Sterna in Längsrichtung flexibel und faltbar sind. — Die abdominalen Stigmen liegen in der Pleuralmembran der Segmente II bis VII (Fig.174).

Das schmale Tergum des 9. Segmentes (Fig.177, TIX) bedeckt als Epandrium die Basis der Gonocoxite (G). An das Tergum schließt sich der Analkomplex mit den langgestreckten Cerci (C) und dem Hypoproct (Hp) an; sie überragen den caudalen Rand der Terminalia.

Caudal schließen sich an die Gonocoxite die Gonostyli (Fig.177, Gs) an. Diese sind rundlich gedrungen ausgebildet, verjüngen sich aber zu einem langgestreckten apikalen Teil, der cranio-dorsad gerichtet ist; dies bedingt, daß von ventral nur der Basalteil der Styli zu erkennen ist (Fig.178). Die Medialseite der Gonostyli ist mit langen, starken mediad gerichteten Borsten besetzt, die sich (in Ruhestellung) reusenartig überkreuzen (Fig.187).

Nach Entfernen von Epandrium und Analkomplex sind die Gonocoxit-Apodeme erkennbar (Abb 179, GA). Diese Erweiterungen des Gonocoxit-Randes verlaufen erst ein Stück craniad, biegen dann aber mediad um.

Penis

Der im cranialen Bereich der Genitalkammer befindliche Penis ist zwischen den Gono-coxit-Apodemen eingehängt und nahtlos mit diesen verbunden (Fig.179). Die Dorsal-seite des Penis zeichnet sich durch die differentiell sklerotisierte Cuticula aus, so daß er sich scheinbar aus mehreren Elementen zusammensetzt (Fig.183). Median befindet sich ein stark sklerotisierter Streifen, der sich als Apodem in das Innere des Penis fort-setzt (medianes Apodem, meA). Caudad erweitert sich diese schmale Zone zu einer ebenfalls kräftig sklerotisierten Platte (dorsale Platte, dPl). Cranial schließen sich an das mediale Apodem die Seitenwände des Penis an (laterale Peniswand, lPw). Sie erstrecken sich halbröhrenförmig bis auf die Ventralseite (s. auch Fig.186a). Caudad verjüngen sich die lateralen Peniswände, die Cuticula zwischen ihnen und medianem Apodem bzw. dorsaler Platte ist membranös differenziert, so daß die sklerotisierten Elemente gegeneinander verschiebbar und beweglich sind. Die Ventralfläche des Penis (Fig.184) wird von den umgreifenden lateralen Peniswänden und einem flachen, annä-hernd dreieckig geformten Sklerit, dem Ejaculator-Apodem (E), gebildet.

Der Ductus ejaculatorius (De) zieht in die Penishöhle hinein und geht dort kontinuier-lich in den Ductus ejaculatorius distalis (Ded) über, ein sackförmiger Endophallus ist nicht ausgebildet. Die Intima des D. e. distalis verbindet ihn nahtlos sowohl mit dem Dorsalsklerit als auch mit dem Ejaculator-Apodem. Zwischen beiden liegt die sekun-däre Geschlechtsöffnung, das Phallotrema (Pt; Fig.188).

Muskulatur

Die Gonostyli werden von zwei Paar antagonistisch wirkender Muskeln bewegt. Der Adduktor (Fig.182, M1) entspringt ventral am cranialen Rand des Genitalsegments, des-sen Boden er großflächig überzieht; die Insertionsstelle dieses Muskels befindet sich basal an der Medialfläche der Gonostyli (Fig.181, M1).

Der schmale Gonostylus-Abduktor (Fig.182, M2) entspringt an der Seitenwand der Gonocoxite und inseriert dorsal an einem basalen Fortsatz der Styli (Fig.180, M2). — Zwischen den Gonocoxit-Apodemen ist ein unpaarer, bogig verlaufender Muskel ausge-spannt (Fig.182, M10); die mediane Ausrichtung der Apodeme bedingt, daß dieser Mus-kel sehr lang ist.

An den Gonocoxit-Apodemen entspringt auch Muskulatur, die zum Funktionskreis des Penis gehört. Ein paariger, breiter Muskel verläuft vom caudalen Abschnitt des Gono-coxit-Apodems zur Ventralseite des Penis; dort inseriert er an der lateralen Peniswand (Fig.182, M11). Bei Kontraktion dieses Muskelpaares wird der Penis nahezu senkrecht aufgerichtet, eine Stellung, die bei fixierten Tieren sehr häufig zu finden ist. Ein weite-res Muskelpaar, das an den Apodemen entspringt, inseriert — ebenfalls auf der Ventral-seite des Penis — am Ejaculator-Apodem (Fig.184, M3). Es fungiert als Retraktor des Ejaculator-Apodems, ein dazu antagonistisch wirkender Muskel ist nicht vorhanden.

Innerhalb der Penishöhle erstreckt sich ein schräg verlaufender Muskel (Fig.183, M9). Er verbindet das mediale Apodem mit der lateralen Peniswand; bei seiner Kontraktion verändert sich der Querschnitt des Penis, und die caudalen Spitzen der lateralen Penis-wand werden einander genähert.

Innere Geschlechtsorgane (Fig.185)

Die langgestreckten, keulenförmigen Hoden (Ho) beginnen im Bereich des 3. abdomi-nalen Segmentes und erstrecken sich bis in das 7. Dort entspringen aus ihnen die dün-

nen, paarigen Vasa deferentia (Vd), die craniad umbiegen und ventral von den Hoden verlaufen, wobei sie direkt nebeneinander liegen. Sie biegen dann wieder caudad um und gehen in die Vesicula seminalis (Vs) über, so daß die Vasa deferentia zwischen Hoden und Vesicula gelegen sind. Aus der Vesicula seminalis geht der dünne, unpaare Ductus ejaculatorius (De) hervor. Akzessorische Drüsen sind nicht vorhanden.

Spermatransfer

Direkte Beobachtungen zum Modus der Spermaübertragung liegen nicht vor, und auch die morphologischen Befunde sind nicht eindeutig interpretierbar. Sicher aber ist, daß der Inhalt des Ductus ejaculatorius distalis durch Bewegungen des Ejaculator-Apodems ausgepreßt wird.

Weibliche Terminalia

Exoskelett

Die weiblichen Terminalia der Diptera bestehen aus den abdominalen Segmenten VIII—XI, die zusammen einen mehr oder weniger langen, teleskopartig einziehbaren Legeapparat bilden (vgl. Fig.189). Da der Terminus „Ovipositor" den orthopteroiden Legeapparat bezeichnet (Snodgrass 1935: 607, 622), dieser aber bei den Diptera bis auf einige Reste reduziert ist (Snodgrass 1935: 608; Mickoleit 1975; McAlpine 1981: 38), wird der Begriff „Ovipositor" in der vorliegenden Arbeit vermieden; statt dessen kommt die ausschließlich deskriptive Bezeichnung „Legeröhre" zur Anwendung.

Die Legeröhre läßt sich in zwei Teilabschnitte differenzieren, nämlich die eigentlichen Genitalsegmente (VIII und IX) und die darauf folgenden Postgenitalsegmente, die die Cerci und den After tragen.

Die Terga der einzelnen Segmente lassen sich gut voneinander unterscheiden, dagegen sind primäre Sterna im Bereich der Legeröhre nicht vorhanden. Dafür befindet sich auf der Ventralseite der Segmente VIII und IX ein Sklerit, dessen unterschiedliche Benennung die Unsicherheit über die Herkunft dieses Elements der Legeröhre widerspiegelt. Da diese „Subgenitalplatte" häufig paarig ausgebildet ist und auch die Grenze des 8. Segments überragt, kann man davon ausgehen, daß sie wenigstens zum Teil den Gonocoxiten des orthopteroiden Legeapparats homolog ist (Smith 1969, Mickoleit 1975, Seather 1977, McAlpine 1981: 44). Es ist aber strittig, welchen Anteil das primäre Sternum VIII am Aufbau des Sklerits hat.

In Anlehnung an Mickoleit (1975), der die entsprechenden Sklerite bei den Mecoptera, dem mutmaßlichen Adelphotaxon der Diptera, als Gonocoxosternite bezeichnete, wird hier dieser Begriff übernommen.

1. Bibioniformia

Zur Bearbeitung der weiblichen Terminalia standen mehrere Arten aus dem umfangreichsten Taxon der Bibioniformia, den **Bibionidae**, zur Verfügung; dokumentiert werden als deren Repräsentanten die Weibchen von *Penthetria funebris* (Pleciinae) und *Dilophus febrilis* (Bibioninae).

Genitalsegmente

Die Ventralseite der Genitalsegmente (Segmente VIII und IX) wird bei *P. funebris* und *D. febrilis* vollständig vom Gonocoxosternit des 8. Segments eingenommen, da dieses

caudad über das Segment VIII hinaus verlängert ist (Fig.189, 192; Gx VIII). Während das Gonocoxosternit bei *P. funebris* durchgehend paarig ist (Fig.191), ist es bei *D. febrilis* als mächtige, unpaare Skleritplatte vorhanden; lediglich caudal befindet sich median ein Einschnitt, so daß es in diesem Bereich paarig erscheint (Fig.194).

An das große Tergum des 8. Segments schließt sich bei *Penthetria* dorsal eine ausgedehnte Conjunctiva an, auf die das viel schmalere Tergum IX folgt (Fig.189, T IX). Im Gegensatz dazu zeichnet sich *D. febrilis* durch eine schmale Conjunctiva aus, die dorsolateral ein Paar Erhebungen aufweist. Hierbei handelt es sich um das 8. abdominale Stigmenpaar, wobei die Öffnung des Stigmas an der Spitze der cuticularen Ausstülpung lokalisiert ist (Fig.192, 193, 195, 196; St VIII).

Das Tergum des 9. Segments ist bei beiden Vertretern der Bibionidae spangenartig schmal und erstreckt sich lateral bis zum dorsalen Rand des Gonocoxosternit (Fig.189, 192, 194; T IX). Es verschmälert sich bei *P. funebris* dorso-medial stark und ist paarig ausgebildet (Fig.190).

Postgenitalsegmente

Nur bei *P. funebris* ist das Tergum des 10. Segments als kleine Skleritplatte erhalten (Fig.190, TX). Bei *D. febrilis* folgen auf das Tergum IX die Cerci (Fig.192, 193); Reste des Tergum X sind nicht erhalten.

Ventral bildet das 10. Segment eine unpaare Platte aus, die sogenannte Postgenitalplatte, die im Falle von *P. funebris* lateral durch eine Membran mit dem Tergum X verbunden ist (Fig.191; Pgp). Bei *D. febrilis* dagegen liegt die Postgenitalplatte ohne tergalen Kontakt ventral von den Cerci (Fig.194).

An das 10. abdominale Segment bzw. an dessen Reste schließen sich die paarigen Cerci an, die bei *P. funebris* zweigliedrig (Fig.189-191; C1, C2), bei *D. febrilis* dagegen nur eingliedrig sind (Fig.192-194, C). — Die insgesamt sehr kurze Legeröhre kann bei beiden Arten teleskopartig in das 7. abdominale Segment eingezogen werden.

2. Mycetophiliformia

Die Erfassung von Merkmalen im Bereich der weiblichen Terminalia innerhalb dieses artenreichen Taxon erfolgte an Vertretern aller höheren Taxa der Mycetophiliformia („Familien" der konventionellen Klassifikation). Im folgenden werden Merkmale des Exoskeletts dieser Arten vergleichend dargestellt.

Genitalsegmente

Auf der Ventralseite des 8. und 9. Segments befindet sich bei allen untersuchten Arten das Gonocoxosternit VIII. Es ist aber — was Ausmaß und Grad der Sklerotisierung betrifft — verschieden ausgebildet.

Bei *Campylomyza flavipes* (Cecidomyiidae) ist das Gonocoxosternit VIII eine ungeteilte Skleritplatte, die lediglich im caudalen Bereich median etwas schwächer sklerotisiert ist (Fig.197, 198; Gx VIII). Im Gegensatz dazu ist bei allen anderen untersuchten Vertretern der Mycetophiliformia das Gonocoxosternit VIII mehr oder weniger deutlich paarig ausgebildet.

Bei den Sciaridae *(Sciara thomae)* ist das Gonocoxosternit in zwei deutlich unterscheidbare Teile gegliedert (Fig.199, 200). Während der craniale Teil medial nur ein Paar schmaler sklerotisierter Streifen aufweist, im übrigen aber membranös differenziert ist, besteht der caudale Teil aus zwei stark sklerotisierten Platten, die median über eine

Membran miteinander verbunden sind. Das Gonocoxosternit insgesamt ist stark verlängert und reicht — bei vollständig ausgestreckter Legeröhre — bis unter die Cerci.

Ähnlich flexibel und weichhäutig sind die Terminalia von *Macrocera maculata* (Mycetophilidae). Bei dieser Art (Fig.210-212) ist der gesamte craniale Bereich des Gonocoxosternit membranös und nur sein caudaler Teil bildet paarige, sklerotisierte Platten aus. Im Gegensatz zu den Sciaridae ragt bei *Macrocera* das Gonocoxosternit aber nicht bis unter die Cerci.

Bei den übrigen der untersuchten Mycetophilidae findet sich das Gonocoxosternit VIII als weniger stark differenziertes Sklerit.

Durchgehend paarig ist es bei *Bolitophila tenella* (Bolitophilinae; Fig.209) und *Cordyla brevicornis* (Mycetophilinae; Fig.218). *Symmerus annulatus* (Ditomyiinae; Fig.206) zeichnet sich durch ein Gonocoxosternit aus, dessen paarige Platten cranial zu einem einheitlichen Rand miteinander verschmolzen sind. Besonders ausgedehnt ist die unpaare craniale Zone bei *Leia winthemi* (Sciophilinae; Fig.215), so daß die Paarigkeit des Gonocoxosternit nur noch caudal erkannt werden kann. — Ein cranialer unpaarer Bereich findet sich auch beim Gonocoxosternit VIII von *Diadocidia ferruginosa* (Diadocidiidae; Fig.202).

Die Terga der Genitalsegmente (T VIII, T IX) sind bei fast allen der untersuchten Arten ausgebildet, lediglich bei *C. brevicornis* (Fig.216, 217) folgen bereits auf das große Tergum des 8. Segments die Cerci; Tergum IX und auch Tergum X sind nicht vorhanden.

Postgenitalsegmente
Das auf die Genitalsegmente folgende Tergum des 10. Segments ist nicht bei allen Mycetophilidae vorhanden. Es fehlt vollständig bei *M. maculata* (Fig.210, 211) und — wie bereits erwähnt — bei einem Vertreter der Mycetophilinae, bei *C. brevicornis* (Fig.216, 217).

Als umfangreiches Sklerit ist das Tergum X nur bei *C. flavipes* (Fig.197) und *D. ferruginosa* (Fig.201) ausgebildet. Eine spangenartig schmale Form hat es dagegen bei *S. thomae* (Fig.199), *S. annulatus* (Fig.204, 205), *B. tenella* (Fig.207, 208) und *L. winthemi* (Fig.213, 214).

Die Cerci sind in der Regel zweigliedrig, eine Ausnahme hiervon bildet lediglich *Diadocidia* (Fig.201-203, C), deren Cerci eingliedrig sind.

Bei *L. winthemi* sind die Grundglieder der Cerci langgestreckt und dorso-cranial zu einer unpaaren Platte verschmolzen; das apikale Glied ist klein und rundlich geformt (Fig.213, 214; C1, C2). Ein ebenfalls langgestrecktes Basalglied findet sich bei *C. brevicornis*, und auch hier ist das apikale Glied ausgesprochen klein ausgebildet (Fig.216, 217).

Im ventralen Bereich der Postgenitalsegmente befindet sich bei allen Mycetophiliformia ein weiteres Sklerit, die sogenannte Postgenitalplatte (Pgp). Bei den Arten, denen das Tergum des 10. Segments erhalten ist, zeichnet sich die Postgenitalplatte durch eine laterale Verbindung mit diesem Tergum aus, so bei *C. flavipes* (Fig.197), *S. thomae* (Fig.199), *D. ferruginosa* (Fig.201), *S. annulatus* (Fig.205), *B. tenella* (Fig.207) und *L. winthemi* (Fig.213). Die Postgenitalplatte sowohl von *M. maculata* (Fig.210, 212) als auch von *C. brevicornis* (Fig.216) liegt dagegen ohne direkten Anschluß an ein tergales Sklerit ventral von den Cerci.

Ausmaß und Form der Postgenitalplatte sind sehr unterschiedlich. Bei der Gallmücke *C. flavipes* bilden Tergum X und Postgenitalplatte einen einheitlich breiten Skleritring

(Fig.197, 198), der ventrale Teil dieses Ringes ragt dabei nicht unter die Cerci. Bei allen anderen Mycetophiliformia ist die Postgenitalplatte caudad verlängert und erreicht wenigstens die Ventralfläche des basalen Cercus-Glieds.

Die Postgenitalplatte von *S. thomae* (Fig.200b) ist nur lateral stärker sklerotisiert, medial ist die Cuticula viel weichhäutiger. Bei anderen Arten der Sciaridae kann dieser mediane Teil völlig membranös sein (und daher leicht übersehen werden). Langgestreckt und einheitlicher sklerotisiert ist die Postgenitalplatte bei *D. ferruginosa* (Fig.202), *L. winthemi* (Fig.213, 215) und *C. brevicornis* (Fig.218). Aber auch eine eher halbkreisförmige Postgenitalplatte tritt innerhalb der Mycetophilidae auf, so bei *S. annulatus* (Fig.205) und *B. tenella* (Fig.207).

Genitalkammer-Dach

Bei den meisten Insekten besitzen die Weibchen eine taschenförmige Einfaltung der Körperwand hinter dem 8. Sternum; dieser Raum wird als Genitalkammer bezeichnet (Snodgrass 1935: 622). Die Öffnung, die diese Genitalkammer mit der Außenwelt verbindet, kann „Vulva" oder „Gonotrema" genannt werden (Snodgrass 1959; McAlpine 1981: 38) und ist hinter dem 8. Segment gelegen.

Auch im Grundmuster der Diptera ist das Gonotrema zwischen dem 8. und 9. abdominalen Segment lokalisiert (Hennig 1973: 230; Matsuda 1976: 351), kann aber durch die Verlängerung des ventralen Skelettelements, des Gonocoxosternit VIII, weiter caudad verschoben sein. Der primäre Gonoporus liegt in der Genitalkammer und markiert die Einmündung des unpaaren Oviductus communis. Außerdem münden eine oder mehrere Spermathecae und eine akzessorische Drüse in die Genitalkammer. Die Öffnungen der beiden letztgenannten Elemente des weiblichen Genitalsystems liegen in der dorsalen Wand der Genitalkammer, im sog. Genitalkammer-Dach (Hennig 1973: 230). In vielen Fällen wird das Genitalkammer-Dach von Skleriten gestützt, die entweder als Reste des Sternum IX gedeutet (Hennig 1973: 230; McAlpine 1981: 44) oder mit Elementen des orthopteroiden Legeapparats homologisiert werden (Seather 1977). Allgemein akzeptiert ist lediglich, daß das Sternum IX bei den Dipteren in hohem Maße abgewandelt und in die Genitalkammer einbezogen ist, aber auch weitgehend reduziert sein kann. Festzuhalten ist, daß das Dach der Genitalkammer häufig Kontaktzonen zum Tergum des 9. Segments aufweist.

In der vorliegenden Bearbeitung gilt das Interesse hauptsächlich der Mündung der Spermathecae im Dach der Genitalkammer. Zur Schaffung einer soliden Datenbasis sind viele Arten der Bibionomorpha auf dieses Merkmal hin untersucht worden; von diesen werden im folgenden Repräsentanten der Bibionidae und aller höherer Taxa der Mycetophiliformia dokumentiert und beschrieben.

1. Bibioniformia

Im Genitalkammer-Dach von *Penthetria funebris* (Pleciinae) fällt ein median liegendes, abgeflachtes Sklerit, die Genitalfurca (Fig.219, Gf), auf. Zwischen den beiden caudad gerichteten Gabelästen dieses Sklerits befinden sich zwei polsterartige Erhebungen (Fig.223), die die Mündungen der Spermathecae (Fig.219, MSpth) und der akzessorischen Drüse (MaD) tragen.

Die Gänge der drei Spermathecae (SpthD) verlaufen bis zum Dach der Genitalkammer getrennt und münden — ebenfalls getrennt voneinander — in einer kleinen taschenför-

migen Einstülpung, die als Bursa copulatrix (Bx) bezeichnet werden kann. Die Bursa copulatrix öffnet sich unpaar im Genitalkammer-Dach (Fig.223).

Es ist an dieser Stelle zu bemerken, daß sich das Vorhandensein einer Bursa copulatrix auf der männlichen Seite, nämlich im Bau der Spermatophore, widerspiegelt (Fig.70, Spe). Die sich während der Kopulation in der Genitalkammer befindende Spermatophore paßt in ihrer Gesamtheit nicht in die viel kleinere Bursa copulatrix; nur der durch die kragenartig erweiterte Spermatophoren-Wand deutlich abgesetzte apikale Teil mit den drei winzigen Anhängen (Korrelation mit den drei Öffnungen der Spermathecae?) wird in die Bursa des Weibchens eingeführt.

Zwischen den beiden polsterartigen Erhebungen des Genitalkammer-Dachs befindet sich die große unpaare Mündung der akzessorischen Drüse (Fig.223, MaD).

Außer der Genitalfurca ist noch ein weiteres, sehr schmales Skleritpaar vorhanden (Fig.219; dorsale Spange, dSp), das medial vom Genitalkammer-Dach ausgehend laterad bis zum ventralen Rand des Tergum IX (T IX) verläuft und mit diesem verbunden ist.

Ähnlich gebaut ist das Genitalkammer-Dach von *Dilophus febrilis* (Bibioninae). Auch hier münden die drei Gänge der Spermathecae getrennt voneinander in eine Bursa copulatrix; die unpaare Öffnung der Bursa ist aber caudad verschoben, so daß sie als terminale Öffnung im Genitalkammer-Dach zu erkennen ist (Fig.224, Bx).

Die akzessorische Drüse mündet unpaar ventral von der Bursa-Öffnung (Fig.224, MaD). — Andere Öffnungen als die der Bursa copulatrix und der akzessorischen Drüse sind im Genitalkammer-Dach der Bibionidae nicht vorhanden, der Oviductus communis mündet immer medial in die Genitalkammer ein.

2. Mycetophiliformia

Das Genitalkammer-Dach der Sciaridae ist median vollkommen membranös, wird lateral aber von spangenförmigen Skleriten abgestützt. Die Genitalfurca (Fig.220, 225; Gf) ist ein langgestrecktes Sklerit, das mit seinen beiden caudad gerichteten Ästen den medianen Teil des Genitalkammer-Dachs umfaßt; hier liegen die Mündungen der Spermathecae und der akzessorischen Drüse. Die Gänge der beiden Spermathecae (Fig.220, SpthD) verlaufen bis unter den unpaaren Teil der Genitalfurca voneinander getrennt, vereinigen sich dann aber zu einem unpaaren Gang, der caudal vom Furca-Sklerit in einem U-förmig gekrümmten Schlitz mündet (Fig.220, 225; MSpth). Caudal dieser Mündung liegt die ebenfalls unpaare Öffnung der akzessorischen Drüse (MaD). Lateral wird der Rand des Genitalkammer-Dachs von einem spangenförmigen Skleritpaar (dorsale Spangen, dSp) gebildet, das in gesamter Länge mit dem Tergum des 9. Segments verbunden ist.

Bei *Campylomyza flavipes* (Cecidomyiidae) ist das gesamte Dach der Genitalkammer weitgehend membranös; die Genitalfurca (Fig.221, Gf) ist klein, ihre lateralen Äste sind nur schwach ausgebildet. Wie bei den Sciaridae vereinigen sich die Gänge der beiden Spermathecae (SpthD) zu einem unpaaren Endabschnitt, der sich caudal vom Furca-Sklerit im Genitalkammer-Dach öffnet (MSpth). Caudal davon befindet sich auf einer rundlichen Erhebung die ebenfalls unpaare Mündung der akzessorischen Drüse (MaD).

Diadocidia ferruginosa (Diadocidiidae) zeichnet sich durch ein Genitalkammer-Dach mit wohlausgebildeten Sklerit-Elementen aus. Die Genitalfurca (Fig.222, Gf) umfaßt einen aufgewölbten membranösen Bereich, in dem drei Öffnungen lokalisiert sind. Die

Gänge der beiden Spermathecae (SpthD) verlaufen getrennt und münden auch getrennt voneinander caudal vom Furca-Sklerit (MSpth). Um diese beiden kleinen Öffnungen herum kann das Genitalkammer-Dach stark aufgewölbt sein, so daß scheinbar eine Bursa-ähnliche Struktur vorliegt; die Öffnung dieses Wulstes ist aber so groß, daß die beiden Mündungen der Spermathecae im Dach der Genitalkammer sichtbar sind. Direkt hinter diesen Öffnungen liegt die unpaare Mündung der akzessorischen Drüse (MaD).

Ähnlich wie bei den Sciaridae sind die dorsalen Spangen (dSp) des Genitalkammer-Dachs langgestreckt und verbinden es mit dem Tergum des 9. Segments.

Alle untersuchten Arten der Mycetophilidae besitzen ebenfalls zwei Spermathecae, deren getrennt verlaufende Gänge nebeneinander — ebenfalls voneinander getrennt — im Dach der Genitalkammer münden. Es ist weder ein unpaarer Endabschnitt der Gänge noch eine Bursa copulatrix ausgebildet.

Die Lage der beiden Öffnungen im Genitalkammer-Dach ist sehr verschieden. Caudad bis zur Endständigkeit verschoben sind sie bei einigen Ditomyiinae, so bei *Australosymmerus nebulosus* (Fig.227), *A. aculeatus* (Fig.228; hier liegen beide Öffnungen terminal an einem langen Fortsatz des Genitalkammer-Dachs) und *Symmerus annulatus* (Fig.229, 230), ferner bei den Sciophilinae *Leia winthemi* (Fig.235) und *Boletina trivittata* (Fig.238).

Auch in der Größe der Mündungen der beiden Spermathecae sind deutliche Unterschiede festzustellen. Auffallend weite Öffnungen der Spermathecae-Gänge finden sich bei *S. annulatus* (Fig.229, 230), *Keroplatus testaceus* (Keroplatinae; Fig.233, 234), *L. winthemi* (Fig.235), *Cordyla brevicornis* (Mycetophilinae; Fig.242, 243) und *Anatella* spec. (Mycetophilinae; Fig.244).

Die Verschiedenheit der Lage der Spermathecae-Öffnungen bringt es mit sich, daß die unpaare Mündung der akzessorischen Drüse (MaD) ebenso unterschiedlich gelegen ist. Nur bei Formen mit median im Genitalkammer-Dach lokalisierten Spermathecae-Öffnungen wie z. B. *Bolitophila tenella* (Bolitophilinae; Fig.231, 232) und *C. brevicornis* (Fig.242, 243), liegt sie caudal hinter diesen. Bildet das Dach der Genitalkammer aber einen Fortsatz aus, auf dem die Spermathecae münden, so liegt die Öffnung des Drüsengangs unter, d. h. dorsal von diesem Fortsatz in der dorsalen Wand der Genitalkammer (z. B. bei *S. annulatus*, Fig.229; *L. winthemi*, Fig.235). Das Genitalkammer-Dach der Mycetophilidae ist großflächiger sklerotisiert als bei den Cecidomyiidae oder Sciaridae. Im Extremfall besteht es aus einer einzigen Platte, so z. B. bei *K. testaceus* (Fig.233) und *Phronia biarcuata* (Mycetophilinae; Fig.239).

Unabhängig von den Unterschieden in der Ausprägung des Genitalkammer-Dachs ist die Anzahl der Öffnungen, die in ihm lokalisiert sind, konstant. Es sind stets drei (Spermathecae und akzessorische Drüse); der unpaare Oviductus communis öffnet sich in keinem Fall in der dorsalen Wand, sondern immer medial in das Lumen der Genitalkammer.

Ausgewählte Merkmale des Thorax und der Extremitäten

Thorakalsklerite und Extremitätenbasis (Coxae)

Der Bau des Thorax hinsichtlich der sklerotisierten Elemente seiner Seitenwand ist für viele Vertreter der Bibionomorpha gut bekannt; zu nennen sind hier die ausführlichen Arbeiten von Crampton (1925) und Shaw & Shaw (1951).

Es hat sich dennoch als notwendig erwiesen, die Thorax-Seitenwand einiger weniger Arten der Mycetophiliformia darzustellen, um auf bislang kaum beachtete Merkmalsausprägungen aufmerksam zu machen und um diese zu dokumentieren. Berücksichtigt werden Vertreter der allgemein als ursprünglich angesehenen Taxa Sciaridae (Fig.246, 251), Diadocidiidae (Fig.247) und Ditomyiinae (Mycetophilidae; Fig.248, 249). Zur vergleichenden Darstellung der Coxen wird noch eine Art der Cecidomyiidae, *Campylomyza flavipes* (Fig.250), herangezogen.

Thorax

Postpronotum (Ppn) und Episternum I (EsI) sind als Elemente des Prothorax immer vorhanden, dagegen ist das Antepronotum nur bei den Sciaridae ausgebildet (Fig.246, Apn).

Die Seitenwand des mächtig entwickelten Mesothorax setzt sich aus mehreren Skleritplatten zusammen. Das Episternum ist in allen Fällen durch eine Naht in Anepisternum (Aes) und Katepisternum (Kes) geteilt. Das Epimeron (Epm; in den Fig.246-249 grau getönt hervorgehoben) erreicht bei den meisten Mycetophiliformia zwischen Katepisternum und Laterotergit (Lat) die Basis des Thorax. Dies gilt auch für die Sciaridae (Fig.246) (bei denen es konstant eine rechtwinkelige Form aufweist), Diadocidiidae (Fig.247) und für *Australosymmerus* (Ditomyiinae; Fig.248). Dagegen ist das Epimeron bei den übrigen Arten der Ditomyiinae, so auch bei *Ditomyia fasciata* (Fig.249), anders ausgeprägt: dieses Sklerit ist hier klein, annähernd dreieckig geformt und wird basal völlig von Katepisternum und Laterotergit umfaßt.

Auf das Laterotergit folgt ein weiteres Sklerit, das große Mediotergit (Met); zwischen diesem und dem mehr oder weniger stark aufgewölbten Scutum (Sc) ist ein Scutellum (Scu) ausgebildet.

An das Postnotum (Latero- und Mediotergit) schließt sich ein Sklerit des thorakalen Endoskeletts, das Postphragma (Pph), an. Bei den Sciaridae (Fig.246) und Diadocidiidae (Fig.247) ragt das Postphragma weit bis in das 1. abdominale Segment, bei den Cecidomyiidae (Fig.250) ist es ebenfalls mächtig entwickelt. Die Ditomyiinae aber und alle übrigen Mycetophilidae zeichnen sich durch ein stark verkürztes Postphragma aus; bei ihnen ragt es lediglich bis unter das Metanotum (Mtn), niemals aber bis in das 1. Segment des Abdomen.

Coxae

Die Coxen aller drei thorakalen Beinpaare (Cx I—III) sind bei den meisten Mycetophiliformia im Verhältnis zur Höhe des Thorax extrem langgestreckt. Dies gilt für die Diadocidiidae (Fig.247), die Ditomyiinae (Fig.248, 249) und alle übrigen Mycetophilidae. Aber auch bei den Sciaridae findet sich diese Merkmalsausprägung (Fig.246). Lediglich die Cecidomyiidae besitzen kurze Coxen. Interessant ist ein Vergleich der relativen Coxen-Länge bei sehr kleinen, annähernd gleichgroßen Arten der Gallmücken und Sciaridae. Selbst winzige Vertreter der Sciaridae — wie z. B. *Caenosciara alnicola*

(Fig.251) — weisen erheblich längere Coxen auf als Cecidomyiidae ähnlich geringer Größe (z. B. *Campylomyza flavipes*, Fig.250).

Tibialorgan

Die Tibia des vorderen, prothorakalen Beinpaares trägt apikal eine besondere Differenzierung, das sog. Tibialorgan (Fig.252). Seine Verbreitung innerhalb der Mycetophiliformia ist schon länger bekannt, es spielt besonders in der Taxonomie der Sciaridae eine wesentliche Rolle (Tuomikoski 1960). Aber über diesen Bereich hinausgehende Informationen wie etwa zu Histologie oder Funktion standen bislang nicht zur Verfügung.

Differenzierungen der Cuticula

Die Lage des Tibialorgans ist bei allen untersuchten Arten identisch; es liegt subapikal auf der Medialseite der Tibia (Fig.252) und ist in beiden Geschlechtern vorhanden. Die Ausprägung des Tibialorgans weist innerhalb der Mycetophiliformia deutliche Unterschiede auf:

Bei den Sciaridae ist das Tibialorgan durch einen grubig eingesenkten Bezirk der Cuticula gekennzeichnet; diese Einsenkung kann eher flach (*Sciara thomae*, Fig.253) oder tiefer (*Lycoriella mali*, Fig.254) ausgebildet sein. Die Borsten, die in dieser Grube stehen, unterscheiden sich in Anordnung, Länge und Dicke von der übrigen Beborstung der Tibia. So fällt das Tibialorgan von *S. thomae* durch eine Ansammlung besonders dicht stehender Borsten, das von *L. mali* dagegen durch wenige sehr kräftige Borsten auf; bei dieser Art ist auch eine annähernd reihige Anordnung der Borsten zu erkennen.

Eine andere Form des Tibialorgans ist innerhalb der Sciaridae weit verbreitet; hier sind die Borsten der Grube dicht aneinanderstehend zu einer kammartigen Reihe angeordnet (*Bradysia paupera*, Fig.255). Der Borstenkamm befindet sich apikal am Grubenrand, die unbehaarte Cuticula der Grube selbst ist von zahlreichen Poren (Po) durchbrochen.

Auch bei den Diadocidiidae findet sich ein Tibialorgan (*Diadocidia ferruginosa*, Fig.256). In einer deutlich von der übrigen Oberfläche abgesetzten Grube stehen Borsten verschiedener Länge, zwischen denen sich noch feine, kurze Härchen befinden. Dies ist auch die bei den Mycetophilidae am häufigsten auftretende Form des Tibialorgans. Sie findet sich bei den meisten Arten der Mycetophilinae (z. B. *Mycetophila fungorum*, Fig.267) und bei denen der konventionell als Sciophilinae zusammengefaßten Taxa (z. B. *Mycomyia bicolor*, Fig.266). Abweichungen von dieser Ausbildung des Tibialorgans lassen sich häufig auf eine andere Anordnung der Borsten, seltener auf eine schwächere Ausprägung der Tibialgrube zurückführen. Manchmal fehlt das Tibialorgan ganz.

So ist bei manchen Vertretern der Ditomyiinae nur ein einzelner Borstenkamm vorhanden (*Australosymmerus, Symmerus annulatus*, Fig.257), anderen Ditomyiinae, z. B. *Ditomyia fasciata*, fehlt das Tibialorgan völlig. Die Bolitophilinae zeichnen sich durch einen abgesetzten Bezirk der Cuticula aus, der nicht nennenswert vertieft ist (*Bolitophila glabrata*, Fig.258). Die Borsten dieses Bereichs sind apikal auf einen auffallenden Borstenkamm ausgerichtet. Auch bei anderen Arten, denen eine deutlich ausgebildete Grube des Tibialorgans fehlt, befindet sich immer über einem apikalen Borstenkamm ein von der übrigen Oberfläche abgesetztes Feld (Fig.265, 268). Besonders auffällig ist dieses Feld bei *Macrocera* (Keroplatinae), da es groß, langgestreckt und völlig kahl ist (Fig.265). Andere Vertreter der Keroplatinae besitzen dagegen ein deutlich grubiges Tibialorgan, in dem alle Borsten gleichlang und bürstenartig dicht nebeneinander ange-

ordnet sind (*Neoplatyura flava*, Fig.261) oder die Borsten aber zu kammartigen Gruppen zusammengefaßt sind (*Platura marginata*, Fig.262; *P. harrisi*, Fig.263, 264). Vielen Keroplatinae aber fehlt ein Tibialorgan.

Die Arten der Gattung *Sciophila* (Sciophilidae) weisen als Besonderheit ein Tibialorgan mit sehr regelmäßigen Strukturen auf; die Borsten, die in der Tibialgrube stehen, sind einheitlich in zwei oder drei regelmäßigen Kammreihen angeordnet (Fig.259-260).

Histologie

Bereits mit einer einfachen Stückfärbung (vgl. Material und Methode) läßt sich nachweisen, daß das Gewebe unter der Cuticula des Tibialorgans besonders differenziert ist. Aufschluß über die Art dieser Differenzierung kann aber erst die Auswertung von Schnittserien bringen. Sagittalschnitte im Bereich des Tibialorgans zeigen deutlich die grubige Einsenkung der Cuticula (Tibialgrube; Fig.269, Tbgr), in der die Anschnitte der Borsten und Haare zu erkennen sind (Fig.270; Bo, Ha). Der Rand der Borstenbecher ist ungleichmäßig erhöht; der dem basalen Teil der Extremität zugewandte Bereich ist sehr viel höher als der gegenüberliegende (Fig.271, Bob). Dies hat zur Folge, daß die Borsten basal nicht gleichmäßig stark abgebogen werden können.

Die Cuticula der Tibialgrube ist viel dünner als die der übrigen Tibia (Fig.269, Cu). Die Epidermis, die außerhalb des Tibialorgans der Cuticula dicht anliegt (Fig.270, Epi), verdickt sich in dessen Bereich auffallend stark, die Epidermiszellen sind hier als hohe Palisaden-Drüsenzellen differenziert (Fig.271, Pz). Dieser Bereich der Epidermis wird nach Weidner (1982: 53) als Drüsenplatte (Fig.269, 270; Dpl) bezeichnet. Zwischen Cuticula und Drüsenplatte befindet sich ein Spaltraum, in den die Zellen ihr Sekret sezernieren (apokriner Typ; Fig.271, Sk). Die dünne Cuticula wird an manchen Stellen von Poren durchbrochen (Po).

Diese Merkmalskombination — dünne Cuticula, Drüsenplatte und Spaltraum — findet sich bei allen untersuchten Arten der Sciaridae, Diadocidiidae und Mycetophilidae, die ein Tibialorgan besitzen, in beiden Geschlechtern. Für die Cecidomyiidae ist niemals ein Tibialorgan beschrieben worden.

REKONSTRUKTION DER STAMMESGESCHICHTE

Die nachfolgende Diskussion befaßt sich mit der Rekonstruktion der Stammesgeschichte der Bibionomorpha und ist in zwei Hauptteile gegliedert. Zuerst wird das Grundmuster der Bibionomorpha für die im deskriptiven Teil erläuterten Merkmalskomplexe rekonstruiert. Flankierend dazu werden weitere, in der Literatur bereits bekannte Merkmale in die Analyse einbezogen werden. Auf der Kenntnis des Grundmusters baut dann im zweiten Teil die Merkmalsbewertung für die Erstellung eines Verwandtschaftsdiagramms der Bibionomorpha auf.
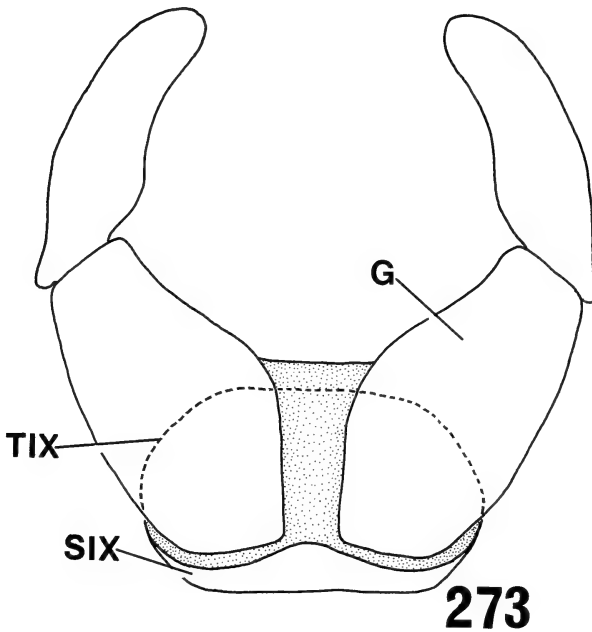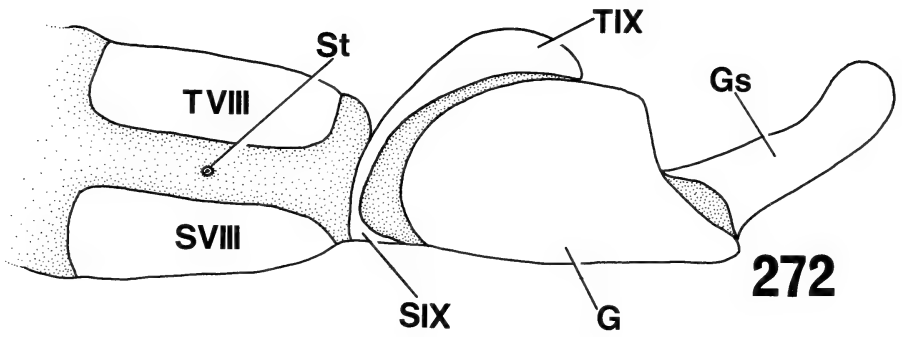
Abb.272-273: Rekonstruktion des Grundmusters der Bibionomorpha, männliche Terminalia: (272) Terminalkomplex, von lateral; (273) Terminalkomplex, von ventral.

Grundmuster-Merkmale der Bibionomorpha

Männliche Terminalia

Die Diskussion der männlichen Terminalia befaßt sich mit der Ausprägung des 8. abdominalen Segments und der nachfolgenden Genitalsegmente im Grundmuster der Bibionomorpha. Da die Genitalsegmente eine funktionelle Einheit bilden, werden sie für die Merkmalsbewertung auch in ihrer Gesamtheit als männliches Genitale diskutiert. Die

Muskulatur wird nicht gesondert behandelt, sondern immer im Zusammenhang mit den zugehörigen Elementen des Exoskeletts betrachtet.

1. Segment VIII

Tergum und Sternum

Bei den meisten Vertretern der Bibionomorpha sind Tergum und Sternum des 8. Segments durch eine Pleuralmembran miteinander verbunden. Diese Merkmalsausprägung ist als Symplesiomorphie anzusehen, die aus dem Grundmuster der Diptera in das der Bibionomorpha übernommen worden ist. Abänderungen sind erst innerhalb der Bibionomorpha entstanden, z. B. die Bildung eines Skleritrings bei *Ditomyia* oder die caudale Verlängerung des Sternum bei allen Mycetophilinae. Sie könnten für die Rekonstruktion der verwandtschaftlichen Beziehungen auf niedrigerem taxonomischem Niveau von Bedeutung sein.

Stigmen des 8. Segments

Während bei den Weibchen vieler Dipteren das 8. Stigmenpaar in seiner ursprünglichen Lage in der Pleuralmembran vorhanden ist, soll den Männchen dieses Paar fehlen (Hennig 1973: 220; McAlpine 1981: 37). Die vollständige Reduktion des 8. abdominalen Stigmenpaares ist nach Hennig (1973: 4) ein abgeleitetes Grundmuster-Merkmal der Diptera. Entgegen dieser Annahme besitzen die Männchen von *Bibio* und *Dilophus* (Bibionidae) acht abdominale Stigmen. Das letzte Paar liegt allerdings nicht in der Pleuralmembran des 8. Segments, sondern ist dorsad und caudad bis an den cranialen Rand des Tergum IX verschoben. Es stellt sich die Frage, ob diese Stigmen ein Neuerwerb innerhalb der Bibionidae sind oder ob die Annahme nicht zutrifft, daß bereits die letzte Stammart der Diptera im männlichen Geschlecht das 8. Stigmenpaar vollständig reduziert hatte.

Für eine Neubildung sprechen die ungewöhnliche Lage des Stigmenpaares und die von den übrigen Stigmen völlig abweichende cuticulare Differenzierung (Lage auf einer Ausstülpung der Cuticula, dichte Behaarung). Die Tatsache, daß *Bibio* und *Dilophus* sich durch eine Reihe abgeleiteter Merkmale auszeichnen und in vielerlei Hinsicht „fortgeschrittener" erscheinen als die übrigen Bibioniformia, sollte nicht als Argument zugunsten der sekundären Ausbildung des Stigmenpaares herangezogen werden, denn auch stark abgeleitete Formen besitzen in aller Regel noch Symplesiomorphien. Eine Argumentationshilfe bieten dagegen die Weibchen der betreffenden Genera; auch sie besitzen ein 8. Stigmenpaar in gleicher Ausprägung und Lage wie die Männchen; das letzte Stigmenpaar ist bislang übersehen worden, weil es nur bei völlig ausgestrecktem Abdomen von außen zu erkennen ist. Da bei weiblichen Dipteren das Vorhandensein von acht Stigmenpaaren keine Seltenheit ist (Crampton 1942), würde man in diesem Fall eher an eine Verschiebung der primären Stigmen als an eine Neubildung zu denken haben. Bei Männchen und Weibchen geht der zuführende Tracheenast des 8. Stigmenpaares — wie bei den übrigen Stigmen auch — von den lateralen Längsstämmen des Systems aus. Die Verlagerung auf die Dorsalseite könnte mit der bei der Kopulation auftretenden Drehung des Terminalkomplexes um 90° zusammenhängen. Die andersartige, viel dichtere Behaarung um die Stigmenöffnung läßt sich einfach mit der Verlagerung von der Pleuralmembran in die Conjunctiva erklären: bei allen abdominalen Segmenten weicht die Pleuralmembran in Dichte und Verteilung der Haare von der Conjunctiva ab.

Ein Blick auf andere Gruppen der Diptera zeigt, daß entgegen der Annahme Hennigs acht abdominale Stigmenpaare auch bei den Männchen anderer Taxa durchaus nicht selten sind. So bildet Reichardt (1929) in einer Arbeit über die männlichen Kopulationsorgane der Asilidae das Abdomen von *Machimus atricapillus* ab; dort sind eindeutig acht Paar abdominaler Stigmen eingezeichnet, und auch im Text wird dieser Umstand ausdrücklich erwähnt. Nach Reichardt besitzen die Männchen von *Asilus* ebenfalls das 8. Stigmenpaar, während die von *Laphria* es reduziert hätten.

Darüberhinaus erwähnt Cook (1981: 335), daß die Imagines der Chaoboridae (Culicomorpha) an den abdominalen Segmenten I—VIII Stigmen besitzen, wobei in dieser Angabe nicht zwischen den Geschlechtern differenziert wird.

Auch für Teilgruppen der Scatopsidae (Psectrosciarinae, Aspistinae) sind im männlichen Geschlecht acht abdominale Stigmenpaare beschrieben (Cook 1963). Da dieses Stigmenpaar — wie bei den Bibionidae — aber nicht in der Pleuralmembran zwischen Tergum und Sternum VIII lokalisiert ist, sondern an den Rand des Tergum IX verschoben ist, scheint Cook es als Neuentstehung innerhalb der Scatopsidae zu betrachten und bezeichnet es als „auxiliary spiracle" (1981: 313).

In der weiteren Außengruppe gehört die Ausstattung mit acht abdominalen Stigmenpaaren in beiden Geschlechtern sowohl zum Grundmuster der Mecoptera (Mickoleit 1975; Willmann 1981) als auch der Siphonaptera (Hopkins & Rothschild 1953: 15, Abb.3).

Aufgrund dieser Merkmalsverteilung ergibt sich folgendes Bild:
Die letzte Stammart der Diptera wies auch im männlichen Geschlecht noch acht abdominale Stigmenpaare auf, der Verlust des 8. Paares ist keine Autapomorphie des Taxon. Dieses Stigmenpaar wurde aber innerhalb der Diptera Veränderungen unterworfen; es ist vielfach unabhängig vollständig reduziert, manchmal — ebenfalls konvergent — dorsad verlagert worden. In seltenen Fällen (Asilidae, Chaoboridae) ist es als Symplesiomorphie an ursprünglicher Stelle erhalten geblieben.

Die Hypothese Hennigs, daß die Reduktion des letzten Stigmenpaares bereits zum Grundmuster der Diptera gehört, läßt sich auf eine Angabe von Crampton (1942) zurückführen, nach der sieben Paar Stigmen die typische Ausstattung der Männchen ist. Hier liegt ein Beispiel dafür vor, daß die weite Verbreitung einer damit für das betreffende Taxon typischen Merkmalsausprägung nicht zwangsläufig ein Indiz für ihren plesiomorphen Charakter ist.

Für das Grundmuster der Bibionomorpha resultiert als Konsequenz, daß sowohl für die Weibchen als auch die Männchen acht abdominale Stigmen angenommen werden müssen. Über die Ausprägung des letzten Stigmenpaares im Grundmuster läßt sich aber keine eindeutige Aussage treffen, da zwei verschiedene Möglichkeiten alternativ denkbar sind. Die erste beinhaltet, daß die letzte Stammart der Bibionomorpha das 8. abdominale Stigmenpaar in seiner ursprünglichen Lage besessen hat, die Verlagerung der Stigmen erfolgte erst innerhalb der Bibionidae. Diese Annahme ist nicht zu belegen, da bislang kein Vertreter der Bibionomorpha mit der plesiomorphen Merkmalsausprägung (Stigmen in der Pleuralmembran) bekannt geworden ist. Andererseits ist denkbar, daß die Verlagerung des Stigmenpaares dorsad und caudad bereits zum Grundmuster der Bibionomorpha gehört; innerhalb des Taxon müßte dieses verlagerte Paar dann mehrfach unabhängig reduziert worden sein; rezent nur noch bei *Bibio* und *Dilophus* vorhanden. Eine Abschätzung der Wahrscheinlichkeit führt zur Annahme der ersten Alternative.

2. Männliches Genitale

Tergum und Sternum IX

Bei allen untersuchten Vertretern der Bibioniformia und Mycetophiliformia ist das Tergum IX caudad verschoben und bedeckt mindestens die Basis der Gonopoden; es ist also (im Wortsinne) als Epandrium ausgebildet. Dagegen finden sich hinsichtlich Ausprägung und Lage des Sternum IX innerhalb der Bibionomorpha einige Unterschiede. Für die Bibioniformia läßt sich sagen, daß das Sternum des 9. Segments als distinktes Element nur noch bei *Cramptonomyia spenceri* (Alexander, 1931) als schmales Sklerit vorhanden ist; diese Spange ist mit dem Epandrium verschmolzen, liegt aber **vor** der Basis der Gonopoden (Wood 1981: 214). Innerhalb der Mycetophiliformia ist das Sternum des 9. Segments als eindeutig erkennbares, distinktes Sklerit bei den Ditomyiinae (Mycetophilidae) vorhanden (*Symmerus annulatus, Australosymmerus fuscinervis* und *A. nebulosus*; nach Munroe (1974) trifft dies auch noch auf weitere Arten beider Genera zu). Wie das Tergum ist es caudad verschoben und liegt ventral der Basis der Gonocoxite.

Während aus der Merkmalsverteilung zwanglos geschlossen werden kann, daß im Grundmuster der Bibionomorpha (Abb.272-273) das Tergum IX caudad verschoben und damit als Epandrium ausgebildet ist, gilt dies nicht für die Ausprägung des dazugehörigen Sternum. Der Außengruppen-Vergleich zeigt, daß bei etlichen nematoceren Diptera das Sternum IX — wenn überhaupt noch vorhanden — mit dem Tergum zu einem Skleritring verschmolzen ist, der vor der Basis der Gonopoden liegt. Dies gilt für *Trichocera* (Trichoceridae, Neumann 1958), *Chironomus* (Chironomidae, Abul-Nasr 1950), Culicidae (Ewards 1920), Simuliidae (Hennig 1973: 209; Peterson 1981: 356), Tanyderidae (Alexander 1981: 150) und *Pericoma* (Psychodidae, Just 1973; „Basalplatte" und „Basalring"). Auch zum Grundmuster der Brachycera gehört ein distinktes Sternum IX. Es ist bei vielen orthorraphen Brachycera („niedere" Brachycera) zu finden, so z. B. bei *Rhagio* (Hennig 1976; Karl 1959; Nagatomi 1984) und anderen Vertretern der Rhagionidae, bei *Dioctria* (Asilidae, Lyneborg 1968) und *Empis* (Empididae, Ulrich 1972). Hennig (1973: 209) hebt besonders hervor, daß bei den orthorraphen Brachycera das Sternum des 9. Segments immer caudad verschoben ist.

In der weiteren Außengruppe liegen im Grundmuster der Mecoptera Tergum und Sternum IX vor der Genitalkapsel, darüberhinaus sind beide zu einem Ring verschmolzen (Willmann 1981a,b). Die Siphonaptera können zu diesem Vergleich nicht herangezogen werden, da sie durch die Einbindung der Sklerite des 8. Segments bereits im Grundmuster stark abgeleitet sind (Cheetham 1988).

Das Vorkommen der Ringbildung von Tergum und Sternum IX in den verschiedenen Großgruppen der Diptera legt den Schluß nahe, daß ein solcher Skleritring, vor der Basis der Gonopoden gelegen, bereits ein Grundmuster-Merkmal der Diptera ist. Besonders gestützt wird diese Hypothese dadurch, daß in der weiteren Außengruppe die Ringbildung im Segment IX ein Grundmuster-Merkmal der Mecoptera (Willmann 1981a) und vermutlich auch der Amphiesmenoptera darstellt: Trichoptera (Malicky 1973: 52) und Lepidoptera (Matsuda 1976: 414).

Diese Argumentation führt zu der Annahme, daß die Lage des Sternum IX vor den Gonocoxiten und seine Verschmelzung mit dem Tergum aus dem Grundmuster der Diptera in das der Bibionomorpha übernommen worden ist, wo diese Merkmalsausprägung durch *Cramptonomyia* noch bei den Bibioniformia repräsentiert ist. Die Merkmalsverteilung bei *Cramptonomyia* belegt, daß Verlagerung und Vergrößerung von Ter-

gum und Sternum IX nicht zwangsläufig synchron verlaufen, und zeigt auch, daß die Ringbildung beider Sklerite während dieses Prozesses beibehalten wird.

Innerhalb der Bibionomorpha ist das Sternum IX dann entweder caudad verlagert oder reduziert worden. *Cramptonomyia spenceri* repräsentiert damit hinsichtlich der Ausprägung von Tergum und Sternum des 9. Segments den Grundmuster-Vertreter der Bibionomorpha.

Bei der Mehrzahl der Bibionomorpha ist das Sternum des 9. Segments distinkt nicht mehr vorhanden. Seine Verlagerung caudad ist die Voraussetzung dafür gewesen, daß es in den eigentlichen Genitalbereich integriert werden konnte. Seine Rolle bei der Bildung der sklerotisierten Ventralfläche des Segments wird daher im nächsten Abschnitt diskutiert.

Gonocoxite und Genitalkammer

Bei allen untersuchten Vertretern der Bibioniformia und Mycetophiliformia sind die Basalglieder der Gonopoden miteinander verbunden. Allen gemeinsam ist der Zusammenhang über eine dorsale Brücke, an die sich caudad der Penis anschließt. Diese Merkmalskonfiguration ist bei allen Diptera mit ausgebildeten Gonocoxiten vorhanden. Darüberhinaus ist eine solche dorsale Verbindung auch in der Außengruppe zu finden; bei den Mecoptera wird sie als „Genitaljugum" bezeichnet (Willmann 1981a, b), bei den Siphonaptera als „pons parameralis" (Günther 1961). Diese Merkmalsverteilung läßt den Schluß zu, daß die dorsale Brücke bereits zum Grundmuster der Diptera gehört und innerhalb des Taxon eine Symplesiomorphie darstellt.

Auf der Ventralseite ist die Verbindung der Gonocoxite sehr vielgestaltig ausgeprägt. Das Spektrum reicht von Formen, bei denen die Coxite durch einen membranösen Bereich weit voneinander getrennt sind (*Pergratospes holoptica*, Bibioniformia; Krivosheina & Mamayev 1970), bis hin zu solchen, bei denen ein einheitlich sklerotisierter Genitalsegment-Boden ausgebildet ist, der kontinuierlich in die Wand der Gonocoxite übergeht; dies ist die bei den Bibionomorpha am häufigsten vorkommende Merkmalsausprägung. Beide Extreme sind über eine Reihe morphologischer Zwischenstufen — nicht Zwischenstufen im phylogenetischen Sinne! — miteinander verbunden, die im folgenden genauer betrachtet werden.

Im Gegensatz zur oben erwähnten *P. holoptica* bilden die Gonocoxite von *Cramptonomyia spenceri* — eine weitere Art der Pachyneuroidea — eine schmale ventrale Brücke aus; sie berühren sich in der Medianen für eine kurze Strecke, divergieren dann aber caudad und sind nicht mehr miteinander verbunden (Wood 1981: 215). Sowohl bei Hesperinidae (Hardy 1945, 1960) als auch bei den Bibionidae ist die ventrale Begrenzung des Genitalsegments — der Raum zwischen den Gonocoxiten — durchgehend sklerotisiert, lediglich median am caudalen Rand befindet sich eine membranöse Zone, die bei *Dilophus* und *Bibio* als äußerst schmaler, membranöser Streifen ausgebildet sein kann.

Diese Schwächezonen in der Cuticula signalisieren nicht unbedingt die ursprüngliche Grenze zwischen den Gonocoxiten; vielmehr ist auch denkbar, daß sie sekundär — einhergehend mit dem Erwerb größerer Flexibilität — entstanden sind. Die Muskulatur der Ventralfläche des Genitalsegments bei *Dilophus* und *Bibio* deutet auf diese Alternative hin (vgl. weiter unten, „Muskulatur").

Innerhalb der Mycetophiliformia sind die Vertreter von *Australosymmerus* (Ditomyiinae) von besonderer Bedeutung, da sich bei ihnen die Integration des Sternum IX in

die Ventralfläche verfolgen läßt. Entsprechend vielfältig ist die Ausprägung der Ventralseite innerhalb dieses Taxon (die folgenden Angaben beziehen sich auf Abbildungen aus der Monographie von Munroe 1974).

Neben Arten, bei denen das Sternum des 9. Segments als deutlich abgegrenztes Sklerit die Basis der Gonocoxite bedeckt (z. B. *A. nitidus* (Tonnoir, 1927), *A. tillyardi* (Tonnoir, 1927)), gibt es solche, bei denen das Sklerit in die Ventralfläche einbezogen ist (Synsklerit-Bildung), aber durch eine Naht oder einen membranösen Streifen deutlich abgesetzt ist (z. B. *A. fuscinervis, A. rieki* (Colless, 1970), *A. stigmaticus* (Philippi, 1865)). In diesen Fällen ist das Sternum häufig sehr klein, so daß es lediglich die Medianfläche des cranialen Bereichs bildet; an das Sklerit schließt sich dann eine membranöse Zone an, die die Gonocoxite miteinander verbindet. Arten, bei denen das Sternum IX nicht mehr eindeutig abgegrenzt werden kann, sind z. B. *A. anthostylus* Colless, 1970.

Ähnliche Verhältnisse — wenn auch nicht ganz so vielfältig — finden sich bei Vertretern von *Symmerus*. So ist bei *S. annulatus* das sehr große Sternum IX vollständig in die ventrale Begrenzung des Genitalsegments integriert.

Durch den Außengruppen-Vergleich wird deutlich, daß die Gonocoxite ventral oft miteinander verbunden sind und daß die Ausprägung dieser Ventralfläche bei den übrigen Dipteren ebenso vielfältig ist wie innerhalb der Bibionomorpha.

Die Unterschiede in der Ausprägung des Bodens des Genitalsegments innerhalb der Diptera kommen dadurch zustande, daß in verschiedenen Taxa unabhängig voneinander eine durchgehend sklerotisierte Ventralfläche evolviert wurde, wobei dies aber auf verschiedenen Wegen geschehen ist. Ein wesentlicher Unterschied betrifft das Sternum IX. Es kann an der Bildung des Bodens beteiligt sein — wie am Beispiel von *Symmerus* und *Australosymmerus* belegt ist —, spielt aber häufig bei diesem Prozeß keinerlei Rolle; dies trifft z. B. auf die Simuliidae (Culicomorpha) zu, bei denen sich die Gonocoxite in der Medianen berühren und so — ohne miteinander zu verschmelzen — die Ventralfläche bilden (Peterson 1981: 357). Bei diesen Formen ist das Sternum IX weitgehend oder vollständig reduziert, Reste liegen als schmale, mit dem Tergum IX verschmolzene Spange vor der Basis der Gonocoxite. Innerhalb der Bibionomorpha kommt diese Merkmalskombination bei *Cramptonomyia spenceri* (Bibioniformia) vor.

Dem Grundmuster der Diptera dürften daher Formen nahestehen, bei denen die Ventralfläche weitgehend membranös ist, die Gonocoxite medial nicht ausgedehnt sind und bei denen gleichzeitig der Skleritring des 9. Segments vor der Basis der Gonopoden liegt; die beiden Elemente des Ringes, Tergum und Sternum, sind nicht caudad verlängert. Rezent ist eine solche Merkmalsausprägung z.T. noch bei den Trichoceridae zu finden. Demgegenüber sind alle Vertreter der Bibionomorpha hinsichtlich des Tergum IX in diesem Merkmalskomplex abgeleitet. Eine durchgehend sklerotisierte Ventralfläche, die lateral kontinuierlich in die Gonocoxite übergeht, ist aber mehrfach innerhalb des Taxon entstanden und gehört nicht — wie die Verhältnisse bei *Cramptonomyia* (Bibioniformia) und Ditomyiinae (Mycetophiliformia) zeigen — zum Grundmuster der Bibionomorpha.

Die Bezeichnung „Sternum IX" für den gesamten ventralen Bereich des männlichen Genitale, wie sie z. B. von Abul-Nasr (1950), Matsuda (1976: 347) und in vielen taxonomischen Arbeiten verwendet wird, ist unglücklich gewählt. Es handelt sich hierbei niemals um das primäre Sternum allein, sondern dieses ist in wechselndem Umfang (oder überhaupt nicht) mit Anteilen der Gonocoxite verwachsen. Damit liegt eine neue, kom-

plexere Struktur (Synsklerit) vor; diesem Umstand sollte terminologisch Rechnung getragen werden.

Zu diskutieren bleibt die Frage nach den funktionellen Gründen für die mehrfache Bildung eines festen Genitalsegment-Bodens innerhalb der Diptera. Neben einer allgemeinen Stabilisierung und Verfestigung des gesamten Terminalkomplexes ist dabei auch an die Funktion der Ventralseite als Ansatzstelle für die Muskulatur der Gonostyli zu denken; der Adduktor, der die Styli (mit denen während der Kopulation der weibliche Partner ergriffen und festgehalten wird) medial einschlägt, entspringt immer auf der Ventralseite des Segments. Durch eine Versteifung des gesamten Bodens wird die Ansatzfläche des Muskelpaares erheblich vergrößert. So ist der Gonostylus-Adduktor bei *Trichocera* in seinem Ursprung auf die sklerotisierte Wandung der schmalen Gonocoxite beschränkt (Neumann 1958), während das Muskelpaar bei Formen mit durchgehend sklerotisierter Ventralfläche diese im Bereich ihres Ursprunges großflächig bedeckt; bei den meisten Bibionomorpha stoßen beide Muskelzüge sogar in der Medianen der Ventralseite, die sie fächerförmig bedecken, zusammen.

Muskulatur, die sich in ihrer Lage (Ursprung und Ansatz) nur auf die Ventralseite beschränkt, ist innerhalb der Bibionomorpha ausgesprochen selten. Sie kommt bei *Australosymmerus* (Mycetophilidae, Ditomyiinae) und innerhalb der Bibioniformia bei *Bibio* und *Dilophus* (Bibionidae) vor.

Der zur Längsachse des Genitalsegments quer verlaufende, unpaare Muskelzug bei *Dilophus* und *Bibio* (M8) hat keine Entsprechung in anderen Taxa der Diptera insgesamt, so daß er als Neuentwicklung innerhalb der Bibionidae angesehen werden muß. Seine Funktion ist nicht völlig klar; während bei *Dilophus* die Kontraktion dieses Muskels die Ventralfläche fast in ganzer Länge dachartig knickt, wird bei *Bibio* lediglich die Spannung der ventralen Conjunctiva, die mit dem Penis verbunden ist, verändert. Bei in Kopula fixierten Individuen ist dieser Muskel stets stark kontrahiert.

Die beiden bei *Australosymmerus* vorkommenden Muskelpaare (M14, M15) stehen in Verbindung mit dem Sternum IX. Da sie innerhalb der Diptera anscheinend auch noch bei Brachycera mit ausgebildeten Sternum IX zu finden sind (Rhagionidae, Hennig 1976; Ovchinnikova 1987), können sie als aus dem Grundmuster der Bibionomorpha übernommene Symplesiomorphie bewertet werden. Mit der Reduktion oder Integration des Sternum IX werden auch diese Muskeln zunehmend reduziert, so daß sie bei der überwiegenden Zahl der Bibionomorpha nicht mehr vorhanden sind.

Im Gegensatz zur Ventralseite ist dorsal nur sehr selten ein Synsklerit ausgebildet. Das hängt damit zusammen, daß das Tergum IX nicht nur allein als dorsale Bedeckung des Genitale fungiert, sondern auch den Analkomplex trägt. Bei Arten der Gattung *Bibio* ist das Tergum IX cranial mit den Rändern der Gonocoxite verwachsen. Weiter fortgeschritten ist die Synsklerit-Bildung bei *Rondaniella dimidiata* (Mycetophilidae, Sciophilinae), da das Epandrium nur noch durch eine Naht von den Gonocoxite getrennt ist (Hutson et al. 1980).

Ein vollkommenes Synsklerit entsteht bei der Bildung einer Genitalkapsel, wobei Dorsal-, Lateral- und Ventralfläche nahtlos ineinander übergehen. Das ist nur innerhalb der Ditomyiinae (Mycetophilidae) zu finden, nämlich bei *Ditomyia fasciata*. Das Tergum IX ist hier nicht an der Bildung der Genitalkapsel beteiligt, sondern es bedeckt deren Basis und trägt den Analkomplex.

Synskleritbildungen der Dorsalseite sind unabhängig voneinander in den verschiedenen Taxa entstanden und gehören nicht zum Grundmuster der Bibionomorpha.

Dorsal entspringt vom medialen Rand der Gonocoxite ein Apodempaar. Diese **Gonoco-xit-Apodeme** sind bei fast allen Vertretern der Bibionomorpha (Ausnahme: Genitalkapsel von *Ditomyia*) vorhanden, wobei allerdings Ausmaß und Form erhebliche Unterschiede zeigen können. Am häufigsten sind stabförmige Gonocoxit-Apodeme, die craniad gerichtet sind und fast den Vorderrand des Segments erreichen. Diese Merkmalsausprägung findet sich sowohl innerhalb der Bibioniformia als auch der Mycetophiliformia. Die Gonocoxit-Apodeme vermitteln die Verbindung zwischen Gonocoxiten und dem Begattungsorgan, das mit seinem dorsalen Element zwischen den Apodemen eingehängt ist. Darüberhinaus bieten sie Ansatzstellen für zahlreiche Muskeln, die funktionell alle dem Begattungsorgan angehören.

Selten sind die Gonocoxit-Apodeme so verkürzt und mit dem Penis verwachsen, daß sie als einzelnes Element nur schwer erkennbar sind (z. B. bei *Bolitophila tenella*).

Ein Außengruppen-Vergleich macht deutlich, daß Gonocoxit-Apodeme in identischer Lage über die Bibionomorpha hinaus zu finden sind. Das trifft besonders auf die orthorraphen Brachycera zu (Hennig 1976; Nagatomi 1984; Ovchinnikova 1987). Gonocoxit-Apodeme sind auch bei den meisten nematoceren Diptera ausgebildet, wobei aber Lage und Ausdehnung nicht immer identisch sind. Bei Vertretern der Culicomorpha — Culicidae (McAlpine 1981: 47) und Chaoboridae (Cook 1981: 337) — und bei den Trichoceridae (Neumann 1958) befinden sich kurze Apodeme dorsal am cranialen Rand der Gonocoxite, so daß auf den ersten Blick keine Ähnlichkeit mit den Apodemen bei den Bibionomorpha festzustellen ist. Bedenkt man aber, daß der dorso-mediale Rand der Coxite ein Kontinuum darstellt, dann spricht ein unterschiedlicher Ursprung der Apodeme innerhalb dieses Kontinuum nicht unbedingt gegen eine Homologie dieser Strukturen innerhalb der Diptera.

Unabhängig davon, ob die letzte Stammart der Diptera bereits Gonocoxit-Apodeme besessen hat oder ob diese erst innerhalb des Taxon entstanden sind, kann gesagt wer-

Tab.1: Vergleich der Muskulatur des männlichen Genitale innerhalb der Bibionomorpha.

	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14	M15	M16	M17
Bibionidae																	
Penthetria	+	+	+	+	+	-	+	-	-	-	+	-	-	-	-	-	-
Plecia	+	+	+	+	+	-	-	-	+	-	+	+	-	-	-	-	-
Dilophus	+	+	+	+	+	-	+	+	-	-	+	-	-	-	-	-	-
Bibio	+	+	+	+	+	-	+	+	+	-	-	-	-	-	-	-	-
Sciaridae	+	+	+	+	+	-	+	-	-	+	+	+	-	-	-	-	-
Cecidomyiidae	+	+	+	+	+	-	-	-	-	+	-	-	-	-	-	-	-
Diadocidiidae	+	+	+	+	+	+	+	-	+	-	-	+	-	-	-	-	-
Mycetophilidae																	
Ditomyiidae																	
Australosymmerus	+	+	+	-	+	-	-	-	-	+	-	+	+	+	+	-	-
Symmerus	+	+	+	-	-	-	-	-	-	-	+	-	-	-	-	-	-
Ditomyia	+	+	+	+	+	-	-	-	-	-	-	-	-	-	+	-	-
Keroplatinae	+	+	+	+	+	+	+	-	+	-	-	+	-	-	-	-	-
Bolitophilinae	+	+	+	+	-	-	-	-	+	-	-	+	-	-	-	-	+
Mycetophilinae	+	+	+	-	-	-	-	-	+	+	+	-	-	-	-	-	-

den: langgestreckte, craniad gerichtete Gonocoxit-Apodeme gehören zum Grundmuster der Bibionomorpha.

In einigen Taxa der Bibionomorpha findet sich ein Muskel, der zwischen Gonocoxit-Apodem und medialer Wand des Gonocoxit aufgespannt ist (M7 bei Bibionidae, Sciaridae, einigen Mycetophilidae; vgl. Tab. 1). Das Vorkommen dieses Muskels sowohl innerhalb der Bibioniformia als auch der Mycetophiliformia macht wahrscheinlich, daß der Besitz dieses Muskelpaares zum Grundmuster der Bibionomorpha gehört. Innerhalb des Taxon ist es dann mehrfach reduziert worden.

Gonostyli

Die beiden Glieder der Gonopoden wirken arbeitsteilig zusammen. Während die Basalglieder, die Gonocoxite, einen Raum bilden, der Ansatzstellen für die Muskulatur bietet und den Penis umschließt, sind die Gonostyli hauptsächlich an der Sicherung der Spermaübertragung beteiligt. Sie dienen in erster Linie als Klammerorgane während der Kopula und sorgen so für die äußere Verklammerung der Partner. Darüberhinaus werden sie häufig zur Nahorientierung (Tasten) am weiblichen Partner bis zur Einnahme der endgültigen Kopulationsstellung eingesetzt (Beobachtungen an Bibionidae, Sciaridae und Mycetophilidae).

Innerhalb der Bibionomorpha sind die Gonostyli meist langgestreckte, einteilige Hohlsklerite mit rundlichem oder abgeflachtem Querschnitt; apikal sind cuticulare Differenzierungen wie Borsten, Dornen und Stacheln ausgebildet (Kontaktstellen zum Kopulationspartner). In manchen Taxa weichen die Styli aber stark von diesem Schema ab. Sie können stark verkürzt sein *(Plecia)*, apikal eingekerbt oder bis zur Basis tief gespalten (*Hesperinus*, Hennig 1973: 31; viele Mycetophilidae) oder durch die Bildung von spangenartigen Anhängen komplex gebaut sein *(Bolitophila)*.

Meistens ist kein besonders differenziertes Gelenk zwischen Gonocoxit und Gonostylus ausgebildet; der Stylus ist über eine straff gespannte Gelenkhaut mit dem Coxit verbunden, so daß die Bewegungsrichtung weitgehend durch den Verlauf der Muskulatur bestimmt wird. Dies ist vor allem bei den kleineren Arten der Fall (gilt also für die Mehrzahl der Bibionomorpha), während bei den größeren Bibionidae deutlich dicondyle Gelenke ausgebildet sind.

In der Außengruppe herrscht der Typ des länglichen, einteiligen Gonostylus vor. Diese Merkmalsausprägung gehört zum Grundmuster der Mecoptera (Willmann 1981a) und wahrscheinlich auch zu dem der Siphonaptera (Günther 1961). Nur in Verbindung mit diesem Befund ermöglicht die weite Verbreitung des langgestreckten, einteiligen Gonostylus innerhalb der Diptera den Schluß, daß es sich hierbei um ein Grundmuster-Merkmal des Taxon handelt. Diese Merkmalsausprägung ist als Symplesiomorphie im Grundmuster der Bibionomorpha beibehalten worden.

Die **Bewegungsmuskulatur** der Gonostyli verläuft innerhalb der Gonocoxite; in die Styli selbst ziehen keine Muskelfasern. Bei den Bibionomorpha sind immer zwei Paar Muskeln — Adduktor (M1) und Abduktor (M2) — ausgebildet. Während der mächtig entwickelte Gonostylus-Adduktor ausnahmslos an der ventralen Wand des Segments entspringt, verläuft der schmalere Abduktor stets dorso-lateral. Sowohl Anzahl als auch Lagebeziehungen dieser Muskeln sind ohne Zweifel Grundmuster-Merkmal der Bibionomorpha. Das Vorkommen dieser Merkmalskombination in anderen Taxa der Dipteren (Trichoceridae, Tipulidae: Neumann 1958; Psychodidae, Ptychopteridae: Just 1973; Brachycera: Bonhag 1950, Hennig 1976, Ovchinnikova 1987) macht wahrschein-

lich, daß diese bereits zum Grundmuster der Diptera gehört. In der weiteren Außengruppe ist die entsprechende Merkmalsausprägung weder für das Grundmuster der Mecoptera noch für das der Siphonaptera bekannt.

Penis

Die bei oberflächlicher Betrachtung auffallende Vielgestaltigkeit des Begattungsorganes innerhalb der Bibionomorpha läßt sich immer wieder auf ein bestimmtes, einheitliches Bauprinzip zurückführen: An die dorsale Verbindung der Gonocoxite zwischen den Gonocoxit-Apodemen (Dorsalbrücke) schließt sich direkt ein zum Penis gehörendes Element, das **Dorsalsklerit**, an. Form und Ausprägung dieses Sklerits können sehr unterschiedlich sein. So reicht die Merkmalspalette von einer durchgehend einheitlich sklerotisierten, halbrunden Platte: Bibioniformia (*Pergratospes*, Krivosheina & Mamayev 1970; *Dilophus, Bibio*), Mycetophiliformia (Cecidomyiidae, Sciaridae, viele Mycetophilidae) bis hin zu einer aus mehreren sklerotisierten Elementen gebildeten, komplexen Struktur bei *Plecia* (Bibionidae). Die Auswertung von Schnittserien hat jedoch gezeigt, daß diese scheinbar gravierenden Unterschiede lediglich auf einer unterschiedlichen Sklerotisierung der Cuticula beruhen, wodurch das Dorsalsklerit in härtere Spangen und dazwischen liegende flexiblere Bereiche aufgeteilt wird.

Häufig ist das Dorsalsklerit nicht nur auf die Dorsalseite beschränkt, sondern greift lateral auf die Ventralseite über, so daß es die Seitenwände eines Hohlraumes bildet.

Die ventrale Begrenzung des Penis stellt sich in Form eines vielgestaltigen, meist aber langgestreckten Sklerits dar. Trotz verschiedener Ausprägung kann die Homologie dieses sog. **Ejaculator-Apodem**s innerhalb der Bibionomorpha gut belegt werden. Es ist immer als Einstülpung des caudalen Randes des Genitalkammer-Bodens, also vermutlich der ursprünglichen Conjunctiva zwischen den Sterna IX und X, aufzufassen; wie das Dorsalsklerit ist es auch an der Bildung der inneren Penisstruktur beteiligt.

Da Dorsalsklerit und Ejaculator-Apodem bei nahezu allen Bibionomorpha vorhanden sind, kann kein Zweifel daran bestehen, daß Dorsalsklerit und Ejaculator-Apodem zum Grundmuster der Bibionomorpha gehören. Darüberhinaus ist das Apodem innerhalb der nematoceren Diptera und orthorrhaphen Brachycera weit verbreitet (McAlpine 1981: 53), so daß es wahrscheinlich ein Grundmuster-Merkmal der Diptera darstellt. Die Zweiteilung des Ejaculator-Apodems in einen stielartigen und einen caudalen verbreiterten Teil ist ebenfalls Grundmuster-Merkmal der Bibionomorpha, denn sie findet sich sowohl innerhalb der Bibioniformia (Bibionidae) als auch der Mycetophiliformia (Cecidomyiidae, Sciaridae, Mycetophilidae). Für Taxa der engeren Außengruppe (Diptera) ist eine solche Zweiteilung noch nicht beschrieben worden.

Ein Dorsalsklerit kommt außerhalb der Bibionomorpha nur noch bei den Blepharicceridae („Tegmen", Zwick 1977) und den orthorrhaphen Brachycera (Nagatomi 1984) vor.

Allen Bibionomorpha ist gemeinsam, daß sowohl Dorsalsklerit als auch Ejaculator-Apodem in direktem Kontakt mit dem Endabschnitt der Ausführgänge, dem Ductus ejaculatorius, stehen und fest mit diesem verbunden sind. Verbindendes Element ist dabei eine dünne, schwach sklerotisierte Lamelle, die als Einstülpung jeweils am caudalen Rand von Dorsalsklerit und Apodem in das Innere des Penis zieht. Diese inneren Lamellen von Dorsalsklerit und Ejaculator-Apodem bilden zusammen mit dem Ductus ejaculatorius eine Einheit.

Im einfacheren Fall geht die Intima des D. ejaculatorius kontinuierlich in die Lamellen des Penis über; das Endstück des D. ejaculatorius wird als D. e. distalis bezeichnet. Die

ectoblastische Herkunft des Ductus ejaculatorius bedingt, daß sein Lumen in ganzer Länge mit einer Intima ausgekleidet ist; im Endabschnitt wird diese Intima aber deutlich dicker, so daß eine gesonderte Bezeichnung dieses Abschnittes möglich und auch gerechtfertigt erscheint.

Eine so geartete Penisstruktur findet sich innerhalb der Bibionomorpha bei Bibionidae, Sciaridae und einigen Mycetophilidae *(Diadocidia, Platyura, Mycetophila)*. Im anderen Fall sind die inneren Lamellen cranial nahtlos miteinander verbunden und umschließen so innerhalb des Penis einen sackförmigen Hohlraum. In diesen Raum, der als Endophallus bezeichnet werden kann (Snodgrass 1935: 589), mündet der Ductus ejaculatorius.

Bei allen Bibionomorpha, die einen Endophallus besitzen (Bibionidae: *Plecia, Dilophus, Bibio*; Cecidomyiidae: *Campylomyza*; Mycetophilidae: *Australosymmerus, Symmerus*), ist dieser nicht ausstülpbar.

Nach Weidner (1982: 224) wird ein nicht ausstülpbarer Endophallus auch als Ductus ejaculatorius distalis bezeichnet. Snodgrass dagegen betonte (1935: 589), daß ein Endophallus auch eine permanent innere Struktur des Penis sein kann.

Abb.274 verdeutlicht, daß sich beide Merkmalsausprägungen nur graduell durch die Lage des Ductus ejaculatorius voneinander unterscheiden. Beim sackförmigen Endophallus mündet der D. ejaculatorius durch die ventrale Lamelle in den Hohlraum. Einen kontinuierlich in die Lamellen des Penis übergehenden Ductus kann man sich durch die Verlagerung seiner Einmündung craniad und durch fortschreitende Verkleinerung des Endophallus denken. Allerdings ist auch die umgekehrte Entwicklung denkbar.
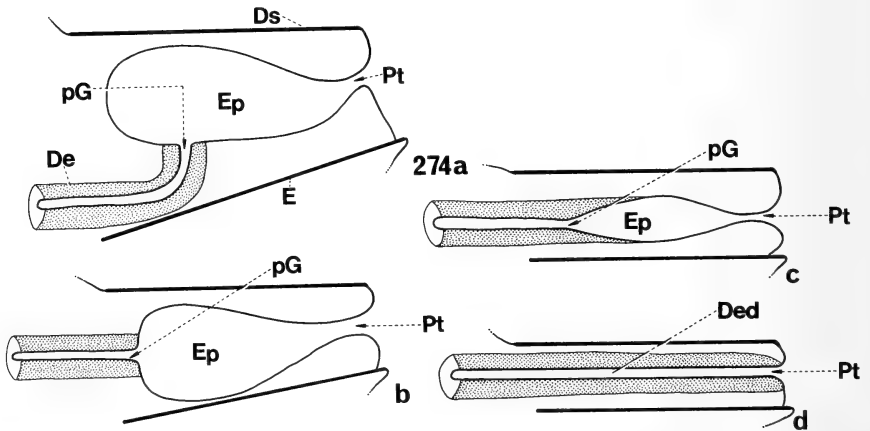
Abb.274a-d: Übergang des Ductus ejaculatorius in das Phallotrema bei Bibionomorpha; (a) Bildung eines sackförmigen Endophallus, der Ductus ejaculatorius mündet ventral ein (Bibionidae, Cecidomyiidae, Mycetophilidae); (b) sackförmiger Endophallus, der Ductus ejaculatorius mündet cranial ein (hypothetisches Zwischenstadium); (c) der Ductus ejaculatorius geht in einen Endophallus über, der primäre Gonoporus (pG) ist aber noch zu lokalisieren (Bibionidae, Mycetophilidae); (d) es ist kein abgrenzbarer Endophallus vorhanden, der Ductus ejaculatorius geht in den Ductus ejaculatorius distalis über (Sciaridae, Mycetophilidae).

Da bei allen untersuchten Bibionomorpha ein innerer Penis-Hohlraum — gebildet aus einem System von Lamellen — vorhanden ist, kann dies als Grundmuster-Merkmal des Taxon angesehen werden. Unklar ist aber, in welcher Ausprägung — Endophallus oder Ductus ejaculatorius distalis — dieses Merkmal im Grundmuster vorliegt.

Bei der Festlegung der Leserichtung ist in diesem speziellen Fall der Außengruppenvergleich nur wenig ergiebig, da interne Substrukturen des Penis nur bei den wenigsten Dipteren überhaupt untersucht sind (die meisten Untersuchungen konzentrieren sich auf das Exoskelett). Ein Endophallus kommt sicher vor bei Chironomidae (Abul-Nasr 1950), Trichoceridae (Neumann 1958) sowie bei orthorraphen Brachycera (Tabanidae: Bonhag 1951).

In der weiteren Außengruppe findet sich im männlichen Genitale der Mecoptera ein Hohlraum, in den der Ductus ejaculatorius mündet (Willmann 1981a). Dieser Raum wird aber von zwei sklerotisierten Genitalfalten gebildet und scheint nicht als eine Einstülpung des Penis aufzufassen zu sein, so daß er mit dem Endophallus der Diptera nicht vergleichbar ist.

Viele Arten der Siphonaptera zeichnen sich durch einen komplex gebauten Endophallus aus, der vom Ductus ejaculatorius durchzogen wird (Günther 1961; Matsuda 1976: 367; Cheetham 1988). Die Ausprägung des Endophallus im Grundmuster der Siphonaptera ist aber noch nicht klar herausgearbeitet worden.

Bei Ausweitung des Außengruppen-Vergleichs von den Antliophora auf deren Schwestergruppe (Amphiesmenoptera [Lepidoptera + Trichoptera]) läßt sich feststellen, daß die Lepidoptera einen Endophallus ausbilden, der dem der Dipteren in Lage und Zusammenhang mit dem Ductus ejaculatorius entspricht (Snodgrass 1937: 602; Tuxen 1956: 102; Matsuda 1976: 415).

Das Vorkommen eines Endophallus in sowohl der engeren als auch der weiteren Außengruppe macht wahrscheinlich, daß es sich hierbei um ein Grundmuster-Merkmal der Diptera handelt, das unverändert in das Grundmuster der Bibionomorpha übernommen worden ist.

Innerhalb der Bibionomorpha sind vereinzelt in manchen Taxa (Bibionidae, Bolitophilinae, Keroplatinae) langgestreckte, paarige Spangen ausgebildet, die zum Penis gehören und als Parameren bezeichnet werden. Auffällig ist in allen untersuchten Fällen der enge Kontakt zum Dorsalsklerit. Es entsteht der Eindruck — vor allem bei *Bibio* und *Platyura* (Keroplatinae) — daß diese Spangen aus der Seitenwand des Dorsalsklerits hervorgegangen sind. Dorsalsklerit und Parameren gehen kontinuierlich ineinander über, eine Grenze zwischen beiden ist nicht erkennbar.

Innerhalb der Diptera ist ein ungegliedertes Spangenpaar, das als Parameren bezeichnet wird, weit verbreitet; es gilt als Grundmuster-Merkmal des Taxon (Hennig 1973: 207; McAlpine 1981: 51). Als Argument für die Homologie dieser Gebilde innerhalb der Diptera wird die Lage der Spangen im Gesamtgefüge des männlichen Genitale angeführt. Die Parameren liegen normalerweise zwischen Gonocoxit und Penis, wobei sie sowohl mit Teilen des Begattungsorgans als auch mit den Gonocoxit-Apodemen verbunden sind (McAlpine 1981: 51). Übereinstimmung in der Lage und die weite Verbreitung innerhalb der Diptera lassen nur den Schluß zu, daß die letzte Stammart der Diptera Parameren besessen hat, da sonst die häufige konvergente Bildung eines Spangenpaares in identischer Lagebeziehung postuliert werden müßte.

Für die Rekonstruktion der letzten Stammart der Bibionomorpha stellt sich die Frage, ob Parameren zum Grundmuster dieses Taxon gehören oder ob paramerenähnliche Spangen innerhalb der Bibionomorpha sekundär evolviert worden sind. Da dieses Problem eng mit der Frage nach der Herkunft des Dorsalsklerits verknüpft ist, wird es im Zusammenhang mit der Entstehung des Penis der Bibionomorpha wieder aufgegriffen und diskutiert.

Die **Muskulatur** des Penis läßt sich ihrer Funktion nach in verschiedene Gruppen einteilen. Es gibt Bewegungsmuskulatur, die das Begattungsorgan insgesamt aufrichten und absenken kann (M4, M11, M12). Daneben sind die Muskeln, die direkt am Ejaculator-Apodem angreifen (M5, manchmal M3), am Auspressen des Spermas (Spermatophore oder freies Sperma) beteiligt. Das gilt auch für die Muskulatur, die direkt am Endophallus inseriert (M3). Entsprechend ihrer elementaren Funktion sind diese Muskeln innerhalb der Bibionomorpha weit verbreitet und in allen höheren Taxa zu finden. Die Homologie der einzelnen Muskelpaare innerhalb der Bibionomorpha ist durch ihre Lagebeziehungen (Ursprung und Ansatz) hinreichend abgesichert.

Die weite Verbreitung dieser Muskulatur läßt darauf schließen, daß es sich hierbei um die Muskeln des Grundmusters der Bibionomorpha handelt. Der zur Absicherung dieser Annahme wünschenswerte Außengruppen-Vergleich muß sich auf einige wenige Taxa der Diptera beschränken, da die Muskulatur des Begattungsorgans nur in sehr wenigen Untersuchungen berücksichtigt worden ist (vgl. Bonhag 1951, Neumann 1958, Ulrich 1972, Just 1973, Hennig 1976 und Ovchinnikova 1987).

Bei den orthorraphen Brachycera finden sich folgende Muskelpaare, die denen der Bibionomorpha sicher homolog sind: M3, M4, M5, und M11 (Bonhag 1951; Ovchinnikova 1987; vgl. Tab. 2). Auch bei nematoceren Dipteren sind Muskeln in gleicher Lage und Funktion vorhanden: M4, M5 und M11 bei Trichoceridae (Neumann 1958) und Ptychopteridae (Just 1973). Auch wenn diese Informationen lückenhaft sind, so stützen sie doch die Hypothese, daß die Bewegungsmuskulatur des Penis zum Grundmuster der Bibionomorpha gehört. Darüberhinaus ist diese Muskelausstattung vermutlich aus dem Grundmuster der Diptera übernommen worden.

Neben dieser Muskelgarnitur kommen innerhalb der Bibionomorpha auch noch weitere Muskeln in Verbindung mit Genitalsegment und Penis vor. In manchen Fällen wird die Innenseite des Dorsalsklerits von Muskelfasern überzogen. Selten verlaufen diese paa-

Tab.2: Muskeln des männlichen Genitale (Grundmuster der Bibionomorpha), die mit Muskulatur anderer Diptera homologisiert werden können.

	Trichoceridae[1]	Blephariceridae[2]	Ptychopteridae[3]	Brachycera[4]	Tabanidae[5]
M1	d	?	M4	M27	M187
M2	e	?	M5	M28	M188
M3	-	-	-	M30	M191
M4	i	3	M3+M10	M2	-
M5	l	5	M11	M31	M193
M11	j	-	M3?	M1	M185
M12	-	+	-	-	-
M15	-	-	-	M33	-

[1] Neumann 1958, [2] Zwick 1977, [3] Just 1973, [4] Ovchinnikova 1987, [5] Bonhag 1951

rig ausgebildeten Muskeln longitudinal (M6 bei Diadocidiidae und Keroplatinae), meist dagegen quer zur Längsachse des Penis (M9 bei Bibionidae, Diadocidiidae, Bolitophilinae, Keroplatinae und Mycetophilinae). Beide Muskelpaare verändern durch ihre Kontraktion den Querschnitt des Dorsalsklerits und damit des Penis insgesamt. Darüberhinaus bewegt das Muskelpaar M9 bei Arten mit Parameren diese Skleritspangen *(Bibio, Bolitophila, Platyura)*. Die Frage, ob der Besitz beider Muskelpaare zum Grundmuster der Bibionomorpha gehört, läßt sich nicht abschließend beantworten. Für den Muskel M9 deutet sein Vorkommen sowohl innerhalb der Bibioniformia als auch der Mycetophiliformia darauf hin, daß ihn bereits die letzte Stammart der Bibionomorpha ausgebildet hatte. Ein weiterführender Vergleich hilft in diesem Fall nicht weiter, da bei anderen Dipteren kein Homologon zu M9 bekannt ist.

Der longitudinal verlaufende Muskel M6 ist nur innerhalb der Mycetophiliformia bei zwei Taxa gefunden worden. Ginge man hier ebenfalls von einem Merkmal aus dem Grundmuster der Bibionomorpha aus, so bedeutete dies die Annahme einer vielfachen Reduktion des Muskelpaares innerhalb der Gruppe. Als Alternative dazu bietet sich die Hypothese an, daß der Muskel M6 erst innerhalb der Mycetophiliformia aus einem anderen Paar hervorgegangen ist. Es könnte sich hierbei um den stark verkürzten und in seinem Ursprung vom Gonocoxit-Apodem auf das Dorsalsklerit verlagerten Muskel M11 handeln. Gestützt wird diese Annahme durch die Tatsache, daß in beiden Fällen, in denen das Muskelpaar M6 ausgebildet ist, das Paar M11 fehlt. Die Homologie der Muskeln M6 und M11 bedeutet, daß M6 nicht zum Grundmuster der Bibionomorpha gehört und erst innerhalb der Mycetophiliformia entstanden ist; ob dies nur einmal oder konvergent geschehen ist, läßt sich nur mit Hilfe des Verwandtschaftsdiagramms der Mycetophiliformia bestimmen.

Zwischen den Gonocoxit-Apodemen befindet sich bei manchen Arten der Mycetophiliformia ein unpaarer Muskel (M10 bei Sciaridae und Mycetophilinae). Auch innerhalb der Ditomyiinae *(Australosymmerus)* kommt dieser Muskel vor, hier verbindet er allerdings die cranialen Apodeme des Dorsalsklerits miteinander. Diese abweichende Lage läßt sich mit der engen räumlichen Beziehung zwischen den Apodemen der Gonocoxite und des Dorsalsklerits erklären. Bei *Australosymmerus* sind die Gonocoxit-Apodeme stark verkürzt und mit dem Dorsalsklerit vollständig verwachsen. Daher kann davon ausgegangen werden, daß diese Muskeln innerhalb der Mycetophiliformia homolog sind.

Innerhalb der Diptera ist ein ebenfalls unpaarer Muskel mit ähnlicher Lagebeziehung nur von *Nephrotoma* (Tipulidae; Snodgrass 1935: 606, Abb.C, Muskel 6) bekannt. In diesem Fall ist er zwischen den cranialen Apodemen der Parameren, die die Seitenwand des Penis bilden, aufgespannt. Dies könnte bedeuten, daß der Muskel M10 bereits ein Grundmuster-Merkmal der Bibionomorpha ist, innerhalb dieses Taxon aber vielfach restlos reduziert wurde. Es besteht aber auch die Möglichkeit, daß der Muskel bei *Nephrotoma* dem der Mycetophiliformia nicht homolog ist. In diesem Fall wäre es dann wahrscheinlicher, daß dieser Muskel erst innerhalb der Bibionomorpha entstanden ist und daher nicht zum Grundmuster des Taxon gehört. — Die Entscheidung für eine der beiden Möglichkeiten ist beim derzeitigen Kenntnisstand nicht möglich.

Die Kenntnis der Muskelgarnitur im Grundmuster der Bibionomorpha ist für die Beantwortung der Frage nach der Herkunft von Dorsalsklerit und Penis insgesamt von großer Bedeutung. Ein Außengruppen-Vergleich zeigt, daß in anderen Taxa der Diptera die Dorsalseite des Begattungsorgans stärker spangenartig gegliedert (z. B. Culicidae:

Ewards 1920; McAlpine 1981: 47, Abb.118; Trichoceridae: Neumann 1958) oder aber auch vollständig membranös (Chironomidae: Abul-Nasr 1950) sein kann. So findet sich innerhalb der Diptera ein weites Spektrum von einem Penis mit einfachem Endophallus und ohne Sklerite (Chironomidae) bis hin zu kompliziert gebauten Penes, die als Spermapumpen fungieren (Trichoceridae, Tipulidae: Neumann 1958; Ptychopteridae, Psychodidae: Just 1973). Auf diese auffallende Vielgestaltigkeit des Begattungsorgans der Diptera ist bereits von van Emden & Hennig (1956: 111) hingewiesen worden.

Für die Entstehung des Dorsalsklerits gibt es zwei Möglichkeiten der Erklärung: Nach der Merkmalsverteilung innerhalb der Diptera kann ein plattenförmiges Sklerit in der Dorsalwand des Penis entweder durch Verschmelzung von mehreren Einzelelementen oder auch als Neubildung entstanden sein. Die Möglichkeit, daß das Sklerit bereits Grundmuster-Merkmal der Diptera ist, kann aus Gründen der Wahrscheinlichkeit außer Acht gelassen werden, weil in diesem Falle multiple Reduktion und Aufgliederung anzunehmen wäre. Ein Vergleich von Merkmalen des Exoskeletts — besonders wertvoll ist in diesem Zusammenhang die detaillierte Arbeit von Neumann (1958) — führt zu dem Schluß, daß das Dorsalsklerit der Bibionomorpha aus den im Grundmuster der Diptera vorhandenen Parameren hervorgegangen ist und keine Neubildung darstellt. Bei den Trichoceridae (Neumann 1958) gehen die Parameren dorsal in eine Platte über („Paramerenbasis"), die lateral paarige, plattenartige Anhänge ausbildet („Flügelplatten"). Paramerenbasis und Flügelplatten sind mit den Gonocoxiten **und** dem Endophallus verbunden.

Wie bereits erwähnt, ist die Verbindung der Parameren mit den Gonocoxiten einerseits und dem Penis andererseits bereits ein Grundmuster-Merkmal der Diptera.

Denkt man sich die beiden Flügelplatten vergrößert, einander genähert und schließlich miteinander verschmolzen, so entsteht ein unpaares Sklerit, das mit den Gonocoxiten verbunden ist und unter dem der Endophallus liegt. Die eigentlichen Paramerenspangen bleiben mit der unpaaren Platte nahtlos verbunden. Da diese Beschreibung genau den Lagebeziehungen des Dorsalsklerits der Bibionomorpha entspricht, erscheint die Bildung des Dorsalsklerits aus Teilen der Paramerenbasis wahrscheinlich.

Das soll aber nicht bedeuten, daß der als Spermapumpe ausgebildete Penis von *Trichocera* direkt als Vorläufer des Begattungsorgans der Bibionomorpha anzusehen ist. Viel-

Tab.3: Vergleich von Funktion und Verlauf (Ursprung und Ansatz) der Penis-Muskulatur bei Bibionomorpha, Brachycera und Trichoceridae (G = Gonocoxit, GA = Gonocoxit-Apodem).

Verlauf	M4	M5	M11
Trichoceridae	Par.basis — G	Par.basis — Kolbenapodem	Par.basis — GA
Bibionomorpha	Dorsalskl. — G	Dorsalskl. — Ejac.- Apodem	Dorsalskl. — GA
Brachycera	Dorsalskl. — G	Dorsalskl. — Ejac.-Apodem	Dorsalskl. — GA
Funktion			
Trichoceridae	Aufrichten	Pumpenmuskel	Zurückziehen
Bibionomorpha	Aufrichten	Pumpenmuskel	Zurückziehen
Brachycera	Aufrichten	Pumpenmuskel	Zurückziehen

mehr sollte an diesem gut untersuchten Beispiel gezeigt werden, daß die Parameren komplex dreidimensional geformt sind und nicht nur ein einfaches Spangenpaar darstellen, das kaum verändert werden kann.

Gestützt wird diese Interpretation durch den Verlauf der Muskulatur des Penis. Das Muskelpaar, das bei *Trichocera* den Penis aufrichtet und wie der Muskel mit entsprechender Funktion bei den Bibionomorpha am medialen Rand der Gonocoxite entspringt, inseriert bei *Trichocera* an der cranialen Apophyse der Paramerenbasis, bei den Bibionomorpha am Dorsalsklerit. Entsprechendes gilt auch noch für zwei weitere Muskeln aus diesem Funktionskreis (vgl. Tab. 3). Alle Muskeln im Penis von *Trichocera*, die sich durch ihre Funktion und Lagebeziehung zu den Gonocoxiten mit Muskeln aus dem Grundmuster der Bibionomorpha homologisieren lassen, inserieren an der Paramerenbasis; bei den Bibionomorpha dagegen inserieren ihre Homologa am Dorsalsklerit. Das läßt sich zwanglos mit einer Enstehung des Dorsalsklerit aus Teilen der Paramerenbasis erklären. Darüberhinaus macht diese Hypothese die enge Lagebeziehung und vor allem die Kontinuität zwischen Dorsalsklerit und Paramerenspangen bei den Bibionomorpha verständlich. Die Parameren der Bibionomorpha sind danach aus dem Grundmuster der Diptera übernommen worden.

3. Innere Geschlechtsorgane

Bei allen untersuchten Bibionomorpha schließen sich an die paarigen Hoden die ebenfalls paarigen Vasa deferentia an. Wie bei fast allen übrigen Dipteren erweitern sich diese zu Vesiculae seminales, die miteinander verschmolzen sind; der paarige Charakter ist aber durchweg erkennbar. Die weite Verbreitung der Vesiculae seminales innerhalb der Diptera und ihr Vorkommen bei fast allen Mecoptera (Kaltenbach 1978: 69) macht wahrscheinlich, daß es sich hierbei um ein Grundmuster-Merkmal der Diptera handelt.

Der Ductus ejaculatorius ist unpaar, nur in wenigen Fällen ist er fast oder gänzlich paarig ausgebildet (Mycetophilidae: bei einigen Ditomyiinae, *Symmerus, Australosymmerus*). Für das Grundmuster der Bibionomorpha kann mit Sicherheit die unpaare Ausprägung des Ductus ejaculatorius angenommen werden, da dies bereits ein Grundmuster-Merkmal der Diptera darstellt (Hennig 1973: 228). Abweichungen von dieser Ausprägung sind erst innerhalb der Bibionomopha entstanden. Sowohl bei Vertretern der Bibioniformia als auch der Mycetophiliformia ist der Ductus ejaculatorius von einer dicken Muskularis, die überwiegend Ringfasern enthält, umgeben. Diese Merkmalsausprägung scheint bereits ein Grundmuster-Merkmal wenigstens der Pterygota zu sein (Snodgrass 1935: 572), so daß sie auch als Symplesiomorphie für das Grundmuster der Diptera angenommen werden kann. Aus dem Grundmuster der Diptera ist sie dann unverändert in dasjenige der Bibionomorpha übernommen worden.

Die Reduktion dieser Muskelschicht ist mit einer Veränderung des Modus des Spermatransfer korreliert. Während bei den Bibionidae, die nachweislich Spermatophoren bilden, eine dicke Muskularis den Ductus ejaculatorius umhüllt, fehlt diese bei den Sciaridae, die Sperma in freier Form übertragen.

Das innerhalb der Bibionomorpha seltener zu findende Paar akzessorischer Drüsen gehört bereits zum Grundmuster der Diptera (Hennig 1973: 228), so daß es innerhalb der Bibionomorpha als Symplesiomorphie bewertet werden kann.

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Zusammenfassung: Die männlichen Terminalia im Grundmuster der Bibionomorpha
— Tergum und Sternum IX bilden einen Sklerit-Ring (Symplesiomorphie); das Sternum liegt als schmale Spange vor der Basis der Gonocoxite (Symplesiomorphie), das Tergum ist dagegen caudad verlängert und als Epandrium ausgebildet (Symplesiomorphie);
— die Gonocoxite sind auf der Ventralseite membranös miteinander verbunden, eine durchgehend sklerotisierte Ventralfläche ist nicht ausgebildet (Symplesiomorphie);
— die Gonostyli sind zylindrisch geformte, ungegliederte Hohlsklerite (Symplesiomorphie);
— die Gonostyli werden von zwei Muskelpaaren, Adduktor und Abduktor, bewegt (Symplesiomorphie); diese Muskeln ziehen nicht in den Stylus, sondern inserieren basal an seiner Medial- und Außenseite (Symplesiomorphie);
— die Gonocoxite bilden dorso-medial ein Apodem-Paar (Gonocoxit-Apodeme) aus, zwischen diesen Apodemen ist der Penis eingehängt (Symplesiomorphie);
— zwischen medialer Gonocoxit-Wand und Gonocoxit-Apodem ist beiderseits ein Muskel (M7) ausgespannt (Autapomorphie ?);
— der Penis besteht aus einer dorsalen Platte („Tegmen", Dorsalsklerit) (Symplesiomorphie) und dem ventral liegendem Ejaculator-Apodem (Symplesiomorphie). Apikal ist zwischen beiden Elementen das unpaare Phallotrema lokalisiert (Symplesiomorphie);
— das Ejaculator-Apodem ist in einen cranialen stielartigen und einen verbreiterten caudalen Teil gegliedert (Autapomorphie);
— ein Paar ungegliederter Anhänge, die Parameren, gehen nahtlos in die Seitenwand des Dorsalsklerits über (Symplesiomorphie);
— innerhalb des Penis befindet sich ein sackförmiger Endophallus, in den der Ductus ejaculatorius einmündet (Symplesiomorphie);
— ein Paar akzessorischer Drüsen mündet ebenfalls in den Endophallus (Symplesiomorphie);
— die Bewegungsmuskulatur des Penis setzt sich aus drei Muskelpaaren zusammen: M4 (Aufrichten des Penis) und M11, M12 (Zurückziehen des Penis) (Symplesiomorphie);
— die Geschlechtsprodukte werden mit Hilfe von zwei Muskelpaaren ausgepreßt: M3 und M5 (Symplesiomorphie);
— die Parameren werden von einem Muskelpaar (M9) bewegt (Autapomorphie ?);
— die inneren Geschlechtsorgane sind in deutlich unterscheidbare Abschnitte gegliedert: paarige Hoden (Symplesiomorphie), paarige Vasa deferentia (Symplesiomorphie), die in die Vesicula seminalis übergehen; der paarige Charakter der Vesicula seminalis ist erkennbar (Symplesiomorphie). Der unpaare Ductus ejaculatorius (Symplesiomorphie) ist von einer dicken Muskularis aus Ringfasern umhüllt (Symplesiomorphie).

Spermatransfer

Bei den Bibionomorpha finden sich verschiedene Modi der Spermaübertragung. Das Spektrum reicht von der Bildung von Spermatophoren im männlichen Genitaltrakt (Bibionidae) über das einfache Auspressen von freiem Sperma (Sciaridae) bis hin zum Spermatransfer mittels komplex gebauter Spermapumpen (Ditomyiinae: *Ditomyia*; Bolitophilinae). Damit stellt sich die Frage, auf welche Weise die letzte Stammart der Bibionomorpha Sperma übertragen hat.

Allgemein wird angenommen, daß bereits im Grundmuster der Diptera die Übertragung freien Spermas verankert ist. Besonders deutlich kommt diese Ansicht in der

Zusammenfassung von Diptera und Mecoptera zu einem Monophylum Antliophora (Pumpenträger) zum Ausdruck (Hennig 1969: 303). Nach Hennig gehört der Besitz einer Spermapumpe zum Grundmuster der Diptera; folgerichtig bewertet er das Auftreten von Spermatophoren innerhalb der Diptera als sekundär (1973: 25). Diese Ansicht ist in neuerer Zeit in das englischsprachige Schrifttum übernommen worden (McAlpine 1981: 53). Ausschlaggebend für diese Festlegung der Leserichtung dürfte sein, daß innerhalb der Diptera bei den im allgemeinen als besonders ursprünglich angesehenen Trichoceridae und Tipulidae Sperma in freier Form übertragen wird (Neumann 1958); hinzu kommt, daß in der weiteren Außengruppe dieser Modus auch zum Grundmuster der Mecoptera (Willmann 1981a) und vielleicht auch der Siphonaptera (Rothschild 1975) gehören soll. Bei näherer Betrachtung fällt der Außengruppenvergleich aber nicht so eindeutig aus. Die Spermapumpe der Mecoptera wurde erst innerhalb des Taxon evolviert (Willmann 1981), und der Modus des Spermatransfer bei der Schwestergruppe zu allen pumpentragenden Mecoptera (Pistillifera, Willmann 1989: 63), den Nannochoristidae, ist unbekannt. Da innerhalb der Mecoptera aber bei den Boreidae Spermatophoren gebildet werden (Mickoleit 1974), ist die Kenntnis des Spermatransfer bei den Nannochoristidae von größter Bedeutung für die Rekonstruktion des Grundmusters. Solange diese Frage nicht beantwortet ist, läßt sich der Modus des Spermatransfer im Grundmuster der Mecoptera nicht schlüssig rekonstruieren.

In diesem Fall erscheint ein weitgefaßter Außengruppenvergleich unumgänglich. Im Zusammenhang mit der Frage nach dem Modus des Spermatransfer im Grundmuster der Diptera hat bereits Pollock (1972) darauf hingewiesen, daß die Bildung von Spermatophoren auch noch für die Pterygota den ursprünglichen Zustand repräsentiert. Dies gilt auch für das Grundmuster der Holometabola, denn innerhalb der Neuroptera, Coleoptera und Hymenoptera kommt die Bildung von Spermatophoren vor (Mann 1984). Darüberhinaus muß auch noch die letzte Stammart der Mecopteroidea Sperma ebenfalls in Form von Samenpaketen übertragen haben, denn nach Mann (1984) stellt innerhalb der Amphiesmenoptera dieser Modus den Regelfall dar. Wegen der Verteilung der Merkmalsausprägungen innerhalb der Mecopteroidea und der Unsicherheiten hinsichtlich des Grundmusters der Mecoptera bietet der Außengruppenvergleich keine Möglichkeit für eine klare Entscheidung zum Grundmuster der Diptera.

So ist die Alternative zur eingangs geschilderten Hypothese zu diskutieren: die Bildung von Spermatophoren ist ein Grundmuster-Merkmal der Diptera und innerhalb des Taxon als Symplesiomorphie zu bewerten.

Innerhalb der Diptera ist die Bildung von Spermatophoren besonders aus der sicher monophyletischen Gruppe der Culicomorpha bekannt (Hennig 1973: 25). Spermatransfer in dieser Form tritt auf bei Chironomidae, Thaumaleidae, Ceratopogonidae und Simuliidae (Downes 1968; McAlpine 1981: 53). Bei den ebenfalls zu den Culicomorpha gehörenden Culicidae fällt dagegen die Übertragung freien Spermas in Zusammenhang mit einem „mating plug" auf; diese Sekretmasse, vom Männchen im weiblichen Genitaltrakt deponiert, wird als Überrest der Spermatophorenbildung gedeutet (Giglioli 1966).

Die Bildung von Spermatophoren ist darüberhinaus auch von Vertretern der Brachycera *(Drosophila, Glossina)* bekannt (Pollock 1972). Dieses Vorkommen ist nicht eindeutig zu interpretieren, da es sich durchaus um sekundäre Bildungen handeln könnte. Es ist aber auch zu bedenken, daß es sich hierbei um außerordentlich gut untersuchte Taxa

handelt; es ist beim derzeitigen Kenntnisstand nicht auszuschließen, daß Spermatophoren innerhalb der Brachycera viel weiter verbreitet sind.

Die Bildung von Spermatophoren ist somit belegt für Culicomorpha, für Bibionomorpha und für einige (stark abgeleitete) Brachycera. Neben diesen Fakten ist noch zu berücksichtigen, daß bei der Übertragung freien Spermas die Pumpen-Einrichtungen innerhalb der Diptera außerordentlich verschieden gebaut sind (vgl. innerhalb der Mycetophilidae *Ditomyia* und *Bolitophila*). Das kann nur bedeuten, daß im Grundmuster der Diptera — im Falle der Übertragung freien Spermas — keine komplexe Pumpen-Einrichtung vorhanden ist. Von einer einfachen „Auspreß-Einrichtung" (Mickoleit 1971) könnten dann verschiedene Spermapumpen, in einigen Taxa aber auch sekundär die Übertragung von Spermatophoren evolviert worden sein. Da der engere Außengruppen-Vergleich (Antliophora) wegen Mangels an Information keinen eindeutigen Hinweis auf das Grundmuster der Diptera liefert, der weitere (Mecopteroidea) aber darauf hindeutet, daß die Bildung von Spermatophoren durchaus Grundmuster-Merkmal der Antliophora und damit auch der Diptera sein könnte, ist folgende Alternative wahrscheinlicher: Die letzte Stammart der Diptera hat Sperma noch in Form von Spermatophoren übertragen; innerhalb des Taxon ist dieser Modus bei Culicomorpha und Bibionomorpha (und Brachycera?) beibehalten worden, in anderen Gruppen wurde die Spermatophore durch den Transfer freien Spermas abgelöst; hierzu sind unterschiedliche Pumpmechanismen evolviert worden.

Beim derzeitigen Kenntnisstand ist die Entscheidung für eine der Alternativen nur über deren Wahrscheinlichkeitsgrad möglich. Die Annahme der Übertragung freien Spermas im Grundmuster der Diptera hat zur Konsequenz, daß innerhalb der Culicomorpha die sekundäre Bildung von Spermatophoren (Grundmuster-Merkmal des Taxon!) wieder rückgängig gemacht wird und durch den Transfer freien Spermas (Culicidae) abgelöst wird. Diese Konsequenz gilt auch genauso für die Bibionomorpha. Insgesamt weist diese Alternative einen geringeren Wahrscheinlichkeitsgrad auf als die Annahme einer Bildung von Spermatophoren im Grundmuster der Diptera.

Die Abschätzung der Wahrscheinlichkeit führt zusammen mit dem weitgefaßten Außengruppen-Vergleich zu der Annahme, daß die letzte Stammart der Diptera Sperma mittels Spermatophoren übertragen hat. Dieser Modus ist unverändert übernommen worden in das Grundmuster der Bibionomorpha.

Weibliche Terminalia

1. Exoskelett (Abb.275-276)

Bei den Weibchen der Bibionomorpha bilden die Segmente VIII bis XI die Legeröhre, wobei in vielen Fällen die Tergite des 8., 9. und 10. Segments erhalten sind (Bibionidae, Cecidomyiidae, Sciaridae, Diadocidiidae und Mycetophilidae). Diese Merkmalsausprägung ist sicher plesiomorph und aus dem Grundmuster der Diptera (Hennig 1973: 218; Seather 1977) in das der Bibionomorpha übernommen worden. Es sind jedoch auch verschieden weit fortgeschrittene Reduktionen von Terga zu finden; besonders betroffen ist dabei das 10. Segment. Bei vielen Arten ist es spangenartig schmal (Sciaridae, Diadocidiidae, Mycetophilidae), bei Weibchen der Pleciinae (Bibionidae) tritt es nur noch als kleines Sklerit an der Basis der Cerci in Erscheinung; vollständig reduziert ist es bei Pergratospes (Pachyneuroidea; Krivosheina & Mamayev 1970), Bibioninae und einigen Mycetophilidae (Keroplatinae, *Cordyla*).

Das Schicksal des Tergum X ist wegen seiner Verbindung mit der **Postgenitalplatte**, einem ventralen Sklerit der Legeröhre, von besonderem Interesse. Bei allen Bibionomorpha, bei denen das Tergum X erhalten ist, besteht zwischen diesem und der Postgenitalplatte eine sklerotisierte Verbindung. Diese Merkmalsausprägung ist darüberhinaus bei allen übrigen nematoceren Dipteren (Seather 1977) und orthorraphen Brachycera (Nagatomi & Iwata 1976, 1978) anzutreffen. In den Fällen, in denen das Tergum des 10. Segments teilweise oder vollständig reduziert ist, verliert auch die Postgenitalplatte den tergalen Kontakt und liegt als isoliertes Sklerit im Ventrum der Postgenitalsegmente. Manchmal ist bei bereits stark reduziertem Tergum X die laterale Verbindung zwischen diesem und der Postgenitalplatte noch vorhanden (*Hesperinus*, Iwata & Nagatomi 1981), bei noch weitergehenden Reduktionen schließt sich lateral an die Postgenitalplatte die Pleuralmembran an (Bibionidae, einige Mycetophilidae).

Die Herkunft der Postgenitalplatte ist bislang kaum diskutiert worden; das hängt damit zusammen, daß sie allgemein entweder als das primäre Sternum des 10. (Hennig 1973: 218; McAlpine 1981: 44) oder des 11. Segments (Seather 1977) angesehen wird. Gegen diese in der Literatur weitverbreiteten Annahmen aber spricht, daß die Postgenitalplatte über das 10. Segment hinausragt und bis unter die Cerci reicht. Die Interpretation von Seather erklärt zwar z.T. die Lage des Sklerits, nicht aber dessen Verbindung zum Tergum X. Es ist in diesem Zusammenhang erwähnenswert, daß meist nur bei Arten mit vollständig reduziertem Tergum X die Postgenitalplatte als Sternum XI, also als Hypoproct, gedeutet wird (z. B. McAlpine 1981: 43, Abb.104-107).

Demgegenüber spricht vieles dafür, daß die Postgenitalplatte aus Elementen des 10. **und** 11. Segments besteht. Auf Gerry (1932) geht die Annahme zurück, daß die Postgenitalplatte aus den Sterna der Segmente X und XI zusammengesetzt ist. Dies erklärt die Lage des Sklerits im Bereich von zwei Segmenten. Die Verbindung zum Tergum X läßt sich auf eine Ringbildung von Tergum und Sternum des 10. Segments zurückführen. In der weiteren Außengruppe findet sich eine solche Ringbildung bei den Mecoptera, und nach Mickoleit (1975) gehört sie bereits zum Grundmuster des Taxon. Eine synapomorphe Übereinstimmung hinsichtlich dieser Merkmalsausprägung bei Mecoptera und Diptera ist wahrscheinlich. In der Stammlinie der Diptera ist dann an den Skleritring des 10. Segments das Sternum XI angeschlossen worden, so daß die letze Stammart der Diptera eine Postgenitalplatte besessen hat. So läßt sich die weite Verbreitung der Platte innerhalb der Diptera und ihr Fehlen in der Außengruppe zwanglos erklären.

Die Postgenitalplatte im Ventrum der Segmente X und XI und ihre Verbindung zum Tergum des 10. Segments gehört auch noch zum Grundmuster der Bibionomorpha; identische Lage des Sklerits im Bereich von zwei Segmenten und die Verteilung des Merkmals innerhalb der Bibionomorpha lassen keinen anderen Schluß zu. Bei Reduktion des Tergum X verliert die Postgenitalplatte ihren tergalen Kontakt und liegt als isoliertes Sklerit vor, das aber dem primären Hypoproct (Sternum XI) nur teilweise homolog ist. Die Entstehung eines sekundären „Hypoproct" in verschiedenen Taxa der Bibionomorpha — verbunden mit der Reduktion des Tergum X — beruht auf Konvergenz.

Die Reduktion von Skleriten ist nicht zwangsläufig mit einer Verkürzung der Legeröhre verbunden, wenn dafür andere Elemente gestreckt und Conjunctivae und Pleuralmembranen erheblich ausgedehnt werden, was die Flexibilität der Legeröhre insgesamt erhöht. Beispielhaft dafür sind die Weibchen von *Cordyla* (Mycetophilidae) und vieler Cecidomyiidae, bei denen einige Arten eine extrem lange Legeröhre ausbilden (Grover 1967; Gagné 1981).

Für die Flexibilität ist auch die Struktur des **Gonocoxosternit** VIII von Bedeutung, das ventral die Begrenzung der Genitalkammer bildet und dessen caudaler Rand die sekundäre Geschlechtsöffnung (Gonotrema) markiert. In vielen Taxa der Bibionomorpha liegt es in paariger Ausprägung vor. Daneben gibt es aber alle Übergänge eines nur teilweise paarigen Gonocoxosternit bis hin zu einer einteiligen, unpaaren Platte. Die Interpretation des Gonocoxosternit als partielles Homologon der paarigen Genitalanhänge des 8. Segments aus dem Grundmuster der Holometabola (orthopteroider Legeapparat; Mickoleit 1975) führt zwangsläufig zur Festlegung der Lesrichtung: der Besitz eines paarigen Gonocoxosternit stellt eine plesiomorphe Merkmalsausprägung dar, die aus dem Grundmuster der Diptera unverändert in das der Bibionomorpha übernommen worden ist. Die Reduktion der Paarigkeit durch zunehmende Verschmelzung beider Platten — beginnend im cranialen Bereich — ist dann vielfach unabhängig innerhalb der Bibionomorpha geschehen. Durch diesen Prozeß wird die Legeröhre ventral stabiler und starrer. Allerdings ist auch der umgekehrte Prozeß denkbar, daß nämlich aus einer unpaaren Platte durch Desklerotisierung in der Medianen sekundär ein paariges Gonocoxosternit entsteht, wodurch die Legeröhre flexibler würde. Die Entscheidung für eine der beiden denkbaren Lesrichtungen ist nur im Einzelfall anhand des Verwandtschaftsdiagramms möglich.

Das **Gonotrema** liegt bei den meisten Bibionomorpha zwischen dem 8. und 9. Segment. Diese Lage ist innerhalb der Diptera als Symplesiomorphie anzusehen (Hennig 1973: 218) und gehört auch noch zum Grundmuster der Bibionomorpha. In der weiteren Außengruppe ist diese Merkmalsausprägung bei den Mecoptera (Grundmuster-Merkmal; Mickoleit 1975) und Siphonaptera (Matsuda 1976: 372) anzutreffen. Innerhalb der Bibionomorpha finden sich Abweichungen von diesem Grundmuster-Merkmal bei den Sciaridae. Bei diesen ist das Gonocoxosternit verlängert, dadurch befindet sich das Gonotrema weiter caudal im Bereich des 10. Segments. Das Gonocoxosternit erscheint deutlich zweigeteilt; cranial von seinem paarigen Teil befindet sich eine ausgedehnte membranöse Zone, deren Cuticula lediglich lateral streifenartig schmal sklerotisiert ist. Seather (1977) homologisiert diesen Teil mit dem Sternum des 8. Segments, der caudale paarige Teil soll den Gonocoxiten des orthopteroiden Legeapparats entsprechen. Damit seien die Sciaridae bezüglich ihrer Legeröhre als besonders ursprünglich anzusehen. Eine entscheidende Konsequenz dieser Interpretation ist, daß durchgehend paarige Gonocoxosternite durch Reduktion des Sternum VIII zustandegekommen sind und daher als abgeleitet bewertet werden müssen.

Bei dieser Argumentation wird aber übersehen, daß bei den Sciaridae das Gonotrema im Bereich des 10. Segments liegt, eine Lage, die zweifelsfrei als apomorph angesehen werden muß. Da das Gonocoxosternit durch seine Ausdehnung die Lage des Gonotrema bestimmt, kann bei den Sciaridae dieses Sklerit nicht in jeder Beziehung den plesiomorphen Merkmalszustand repräsentieren: wenigstens seine Länge muß abgeleitet sein. So ist zusätzlich anzunehmen, daß sich Sternum und Gonocoxite VIII gleichmäßig gestreckt haben und daß dadurch das Gonotrema caudad verschoben worden ist.

Die alternative Hypothese geht davon aus, daß bereits im Grundmuster der Diptera nicht mehr zwischen Sternum VIII und paarigen Anhängen differenziert werden kann; hier liegt eine paarige Struktur vor, bei der die Anteile von Sternum und Coxiten im einzelnen nicht mehr festzustellen sind; sie wird deswegen als Gonocoxosternit bezeichnet. Diese Interpretation läßt sich mit Hilfe des Außengruppenvergleichs stützen. Im Grundmuster der Mecoptera befindet sich im Ventrum des 8. Segments ein durchge-
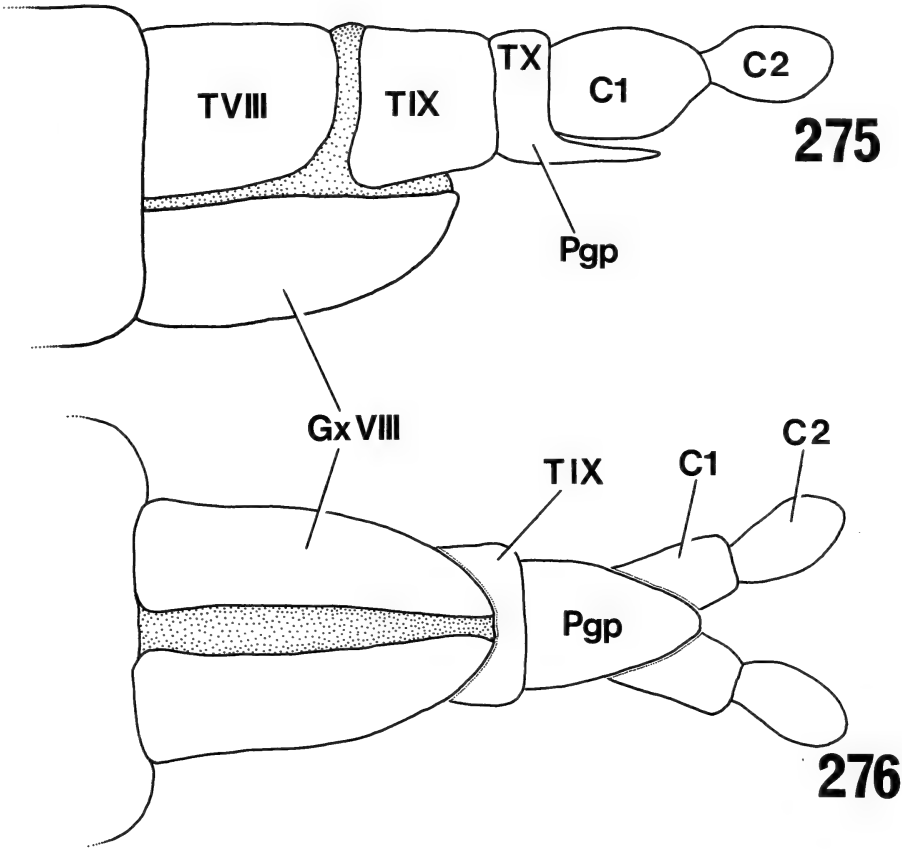
Abb.275-276: Rekonstruktion des Grundmusters der Bibionomorpha: Legeröhre; (275) von lateral; (276) von ventral.

hend paariges Sklerit, das Gonocoxosternit VIII. Erst innerhalb der Mecoptera wird das gesamte Ventrum VIII verlängert, so daß das Gonocoxosternit bis an das Hinterende des 9. Segments verschoben wird. Dabei wird zwischen Sternum VII und Gonocoxosternit VIII eine weitgehend membranöse Zone ausgebildet, in die — bei entsprechender Ausdehnung — das 9. Segment teleskopartig eingezogen werden kann (Mickoleit 1975). An dieser Festlegung der Lesrichtung bestehen keine Zweifel, da das zugrunde liegende Verwandtschaftsdiagramm der Mecoptera durch andere Merkmalskomplexe (männliche Terminalia, Willmann 1981b) bestätigt werden konnte. Innerhalb der Mecoptera wird also ein Merkmalszustand evolviert, wie er auch innerhalb der Diptera bei den Sciaridae zu finden ist.

Die Kenntnisse über das Grundmuster der Siphonaptera sind noch mangelhaft, so daß dieses Taxon nur bedingt zu einem Außengruppenvergleich herangezogen werden kann; dies gilt besonders für Merkmale der weiblichen Terminalia. Es findet sich in der umfangreichen taxonomischen Literatur aber kein Hinweis darauf, daß bei Flöhen die

ventrale Platte des 8. Segments (Subgenitalplatte) zweiteilig, also in Sternum und Coxite differenziert ist.

Merkmalsausprägung und Merkmalsverteilung in der Außengruppe machen wahrscheinlich, daß die mit einer Verlängerung verbundene Zweiteilung des Gonocoxosternit VIII bei den Sciaridae genauso zu bewerten ist wie bei den Mecoptera. Es handelt sich hierbei um eine sekundäre Erscheinung, durch die die Genitalsegmente der Legeröhre gestreckt und das Gonotrema dem Ende der Legeröhre genähert wird. Diese Entwicklung geht von einem durchgehend paarigen Gonocoxosternit aus, das bereits zum Grundmuster der Antliophora gehört und unverändert in das der Mecoptera und Diptera (und Siphonaptera?) übernommen worden ist.

Das Ende der Legeröhre bilden die stets reichlich beborsteten Cerci. Bei den meisten Bibionomorpha sind sie zweigliedrig, vereinzelt kommen aber auch eingliedrige Cerci vor (Bibioninae, Diadocidiidae). Die Zweigliedrigkeit der Cerci ist nach Hennig (1973: 218) ein autapomorphes Grundmuster-Merkmal der Diptera, so daß diese Merkmalsausprägung innerhalb der Bibionomorpha als Symplesiomorphie anzusehen ist.

Insgesamt betrachtet entspricht die Legeröhre im Grundmuster der Bibionomorpha (Abb.275, 276) hinsichtlich ihres Exoskeletts (Erhalt der Tergite VIII—X, paariges Gonocoxosternit VIII, Lage des Gonotrema, Postgenitalplatte und zweigliedrige Cerci) dem Grundmuster der Diptera.

2. Genitalkammer-Dach

Die Wände der Genitalkammer sind membranös, lediglich dorsal finden sich sklerotisierte Elemente. Innerhalb der Bibionomorpha weit verbreitet ist ein gabelförmiges Sklerit, die **Genitalfurca**. Ihr unpaares Ende weist craniad, die beiden Gabeläste sind caudad gerichtet. Diese stützen lateral den Bereich des Genitalkammer-Daches, in dem Spermathecae und akzessorische Drüsen münden. Der umfassenden Bearbeitung der weiblichen Terminalia der Diptera durch Seather (1977) kann entnommen werden, daß die Genitalfurca in allen Großgruppen der nematoceren Diptera zu finden ist. Darüberhinaus ist dieses Sklerit auch bei orthorraphen Brachycera ausgebildet (*Rhagio*, McAlpine 1981: 41, Abb.94). Möchte man nicht die häufige konvergente Bildung eines Furcaähnlichen Sklerits innerhalb der Diptera annehmen, so bleibt nur die Hypothese, daß bereits die letzte Stammart der Diptera eine Genitalfurca im Dach der Genitalkammer besessen hat. Aus dem Grundmuster der Diptera ist diese Merkmalsausprägung in dasjenige der Bibionomorpha übernommen worden.

Die Herkunft der Genitalfurca wird kontrovers diskutiert. Neben der Auffassung, daß es sich hierbei um Reste des primären Sternum IX handelt (Hennig 1973: 230; McAlpine 1981: 44), wird auch die Meinung vertreten, die Sklerite seien Teilen des orthopteroiden Legeapparats homolog (Smith 1969, Seather 1977). Darüberhinaus liegt es aber auch durchaus im Bereich des Möglichen, daß in der dorsalen Wand der Genitalkammer sekundär sklerotisierte Bereiche entstehen, da die Genitalkammer eine Einstülpung der Conjunctiva und damit ectoblastischer Herkunft ist. Mickoleit (1976) konnte nachweisen, daß ein gabelförmiges Sklerit (Medigynium) sekundär innerhalb der Mecoptera gebildet wurde; es ist der Genitalfurca der Dipteren in Form und Lage täuschend ähnlich.

Eine Entscheidung für eine der drei genannten Möglichkeiten ist bei dem derzeitigen Kenntnisstand nicht möglich, für die Rekonstruktion der Stammesgeschichte der Bibionomorpha aber auch nicht unbedingt nötig.

Die Mündung der Spermathecae und der akzessorischen Drüsen im Dach der Genital-kammer ist eindeutig eine Symplesiomorphie, die aus dem Grundmuster der Diptera (Hennig 1973: 218) in das der Bibionomorpha übernommen worden ist.

Innerhalb der Bibionomorpha finden sich hinsichtlich der Anzahl der **Spermathecae** deutliche Unterschiede. Während bei den Mycetophiliformia maximal zwei Spermathe-cae ausgebildet sind, weisen die Bibionidae meistens drei, in seltenen Fällen zwei (*Plecia nearctica*, Leppla 1975) auf. Über die Spermatheken der vier Arten der Pachyneuroidea ist leider nichts bekannt. Um die Anzahl der Spermathecae im Grundmuster der Bibio-nomorpha bestimmen zu können, soll im folgenden ein Außengruppenvergleich vorge-nommen werden.

Innerhalb der Diptera ist die Anzahl der Spermathecae überraschend vielfältig, wäh-rend bei den übrigen Insekten in aller Regel (Ausnahmen bei Blattodea, Saltatoria, Phasmida, Mallophaga, Siphonaptera: Weidner 1982: 235) nur eine Spermatheca vor-handen ist (Snodgrass 1935: 566).

In den verschiedenen Großgruppen der Diptera kommen ein bis vier Spermatheken in scheinbar regelloser Verteilung vor (vgl. Tab. 4). Ein Rückschluß auf die Anzahl der Spermathecae im Grundmuster der Diptera erscheint daher äußerst schwierig. Ein weit-gefaßte Außengruppen-Vergleich zeigt, daß innerhalb der Hexapoda der Besitz von einer Spermatheca als ursprünglich zu bewerten ist. Träfe dies auch für das Grundmu-ster der Diptera zu, dann folgte daraus zwingend die Annahme einer häufigen, konver-genten Vervielfachung der Spermatheken innerhalb dieses Taxon. So sind bei den sicher monophyletischen Culicoidea (Hennig 1973: 25) sowohl Arten mit nur einer als auch

Tab.4: Anzahl der Spermathecae in verschiedenen Taxa der Diptera.

	Anzahl	**Beschreibung**
Perissommatidae	2	Colless (1962)
Anisopodidae	1(2)	Abul-Nasr (1950)
Trichoceridae	3	Downes (1968), Neumann (1958)
Scatopsidae	1	Seather (1977)
Blephariceridae	3	Downes (1968), Seather (1977)
Tipulidae	3	Downes (1968), Seather (1977)
Tanyderidae	3	Downes (1968)
Ptychopteridae	2-3	Seather (1977)
Psychodidae	1-2	Downes (1968), Hennig (1973:24)
Culicidae	3	Downes (1968)
Anopheles, Uranotaenia, einige *Aedes*	1	Downes (1968)
Chaoboridae	3	Seather (1977)
Dixidae	1	Seather (1977)
Simuliidae	1(3)	Downes (1968), Hennig (1973:231)
Ceratopogonidae	1-3	Seather (1977)
Chironomidae	3	Seather (1977)
Bibionidae	3	Seather (1977)
Cecidomyiidae	2	Seather (1977)
Sciaridae	2	Seather (1977)
Diadocidiidae	2	
Mycetophilidae	2	
Asilidae	3	Pollock (1972)
Phoridae	3	Disney (1986)

solche mit drei Spermatheken vertreten, ähnliches gilt auch für die Brachycera (1-4!) und viele andere Taxa (vgl. Tab. 4). Diese Entwicklung ist zwar möglich, aber unwahrscheinlich.

Auf der anderen Seite sind Fälle bekannt, in denen die Annahme einer **Reduktion** von Spermathecae gut begründet erscheint. So besitzen die Weibchen der Simuliidae nur eine Spermatheca, aber daneben noch zwei blind endende Gänge. Diese können als zu Drüsen umgebildete Spermathecae gedeutet werden (Hennig 1973: 231). Ein weiteres Beispiel bieten die Cecidomyiidae; innerhalb der Mycetophiliformia sind es gerade diese kleinen Formen, die häufig nur eine anstatt zwei Spermathecae besitzen (Grover 1967). Eine Korrelation zwischen Verringerung der Körpergröße und Reduktion von Spermatheken könnte auch für die Scatopsidae, die ebenfalls sehr klein sind und nur eine besitzen, angenommen werden. Aus diesen Gründen ist die Annahme am wahrscheinlichsten, daß die letzte Stammart der Diptera drei Spermathecae besessen hat (Downes 1968). Innerhalb der Diptera muß es dann mehrfach zu Reduktionen, punktuell (innerhalb der Brachycera) auch zu einer weiteren Erhöhung der Anzahl gekommen sein. Innerhalb der Bibionomorpha wären die Bibioniformia mit drei Spermathecae im Grundmuster somit ursprünglich geblieben, während die Mycetophiliformia ausnahmslos durch den Besitz von maximal zwei Spermathecae gekennzeichnet sind.

Die langgestreckten und englumigen Gänge der Spermathecae können auf verschiedene Weise im Dach der Genitalkammer münden (Abb.277). Bei den Bibionidae münden sie getrennt voneinander in eine kurze Bursa copulatrix, die sich unpaar im Dach der Genitalkammer öffnet. Dagegen konnte bei den Mycetophiliformia keine Bursa nachgewiesen werden. Eine ähnliche Struktur entsteht aber bei Cecidomyiidae und Sciaridae durch die Vereinigung der Endabschnitte der Gänge zu einem unpaaren Ductus, der sich im Genitalkammer-Dach öffnet (Seather 1977). Bei allen übrigen Vertretern der Mycetophiliformia verlaufen die Gänge der beiden Spermathecae getrennt bis zum Genitalkammer-Dach und münden dort nebeneinander.

Eine ähnliche Vielfalt ist bei den übrigen Dipteren zu finden. Neben der Ausbildung eines unpaaren Endabschnitts oder einer Bursa copulatrix (Tipulidae, Seather 1977, Frommer 1963; Trichoceridae, Chaoboridae, Ceratopogonidae, Seather 1977; Simuliidae, Wenk 1965, Jobling 1987: 79, Abb.229; Culicidae, Brelje 1924; Jobling 1987: 63, Abb.172; Tabanidae, Jobling 1987: 98, Abb.228; Asilidae, Reichardt 1929), kommen auch vollständig getrennt und offen im Genitalkammer-Dach mündende Gänge vor (Trichoceridae, Neumann 1958; Blephariceridae, Seather 1977). Das Beispiel der Asilidae zeigt, daß die Unterscheidung zwischen der Ausprägung eines gemeinsamen unpaaren Ausführganges und dem Vorhandensein einer Bursa copulatrix nicht immer eindeutig möglich ist. Nach Reichardt (1929) vereinigen sich die drei Gänge der Spermathecae bevor sie in die schlauchförmige Bursa copulatrix münden. Ähnliches findet sich auch innerhalb der Tipulidae. Während bei einigen Arten die drei Gänge getrennt voneinander in eine Bursa münden (Frommer 1963), vereinigen sie sich bei anderen Arten teilweise vor der Einmündung (Rees & Ferris 1939; Neumann 1958). Dies bedeutet, daß Bursa und unpaarer Endabschnitt sich nur graduell durch die relative Lage der Spermatheca-Gänge unterscheiden (Abb.277a-d). Ihre Funktion ist identisch, sie bilden beide innerhalb der Genitalkammer einen engeren Vorraum zu den Öffnungen der Spermatheca-Gänge und dienen damit der Sicherung der Spermaübertragung. Am weitesten verbreitet ist innerhalb der Diptera die Bildung eines unpaaren, mehr oder weniger langgestreckten Vorraumes, der der eigentlichen Mündung der Spermatheca-Gänge vorgeschaltet ist und als Einstülpung des Genitalkammer-Daches aufgefaßt werden

kann. Rückschlüsse auf das Grundmuster der Diptera sind allein aus der Verteilung der verschiedenen Merkmalsausprägungen zwar möglich, sollten aber noch durch weitere Argumente gestützt werden.

In diesem Fall kann der Außengruppenvergleich bei der Rekonstruktion der letzten Stammart der Diptera nur bedingt helfen, da im Grundmuster der Mecoptera (Micko-leit 1976) und vermutlich auch der Siphonaptera (Matsuda 1976: 371) nur eine Spermat-heca vorhanden ist. Allerdings sind bei den Flöhen etliche Arten bekannt, bei denen die Weibchen zwei Spermathecae besitzen (Wagner 1939, Snodgrass 1946) oder bei
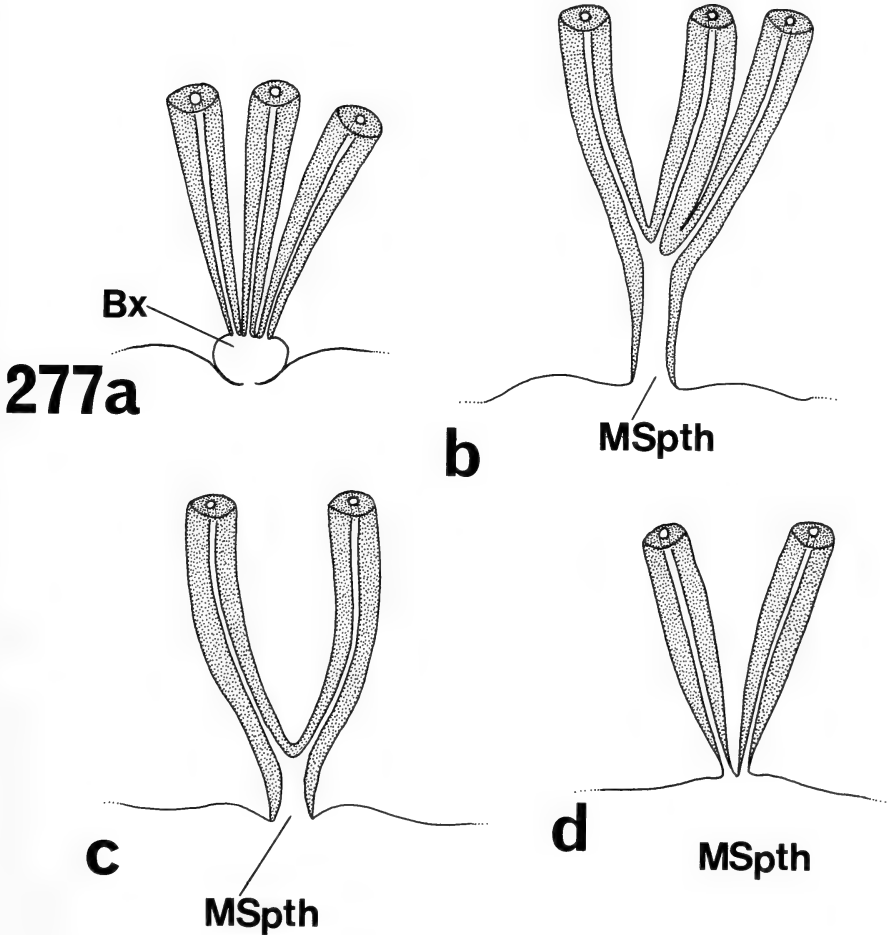
Abb.277a-d: Mündung der Spermathecae im Dach der Genitalkammer: (a) die Gänge der drei Spermathecae münden getrennt in eine Bursa copulatrix (Bibionidae); (b) die drei Gänge vereini-gen sich zu einem unpaaren Endabschnitt (z. B. Asilidae); (c) die Gänge der zwei Spermathecae vereinigen sich zu einem unpaaren Endabschnitt (Cecidomyiidae, Sciaridae); (d) beide Gänge der Spermathecae münden getrennt im Dach der Genitalkammer.

denen die zweite Samenkapsel bis auf ihren Gang reduziert ist (Dampf 1912). In allen diesen Fällen münden die Gänge der Spermathecae in eine Bursa copulatrix, wobei sie sich zu einem unpaaren Endabschnitt vereinigen. Ob die Ausbildung einer Bursa copulatrix bereits zum Grundmuster der Siphonaptera gehört (Matsuda 1976: 272), ist unklar. Sicher ist dagegen, daß die Mecoptera keine Bursa copulatrix aufweisen (Mickoleit 1976). So ist aus dem Außengruppenvergleich lediglich die bei den Siphonaptera auftretende Korrelation zwischen dem Besitz von zwei Spermathecae und der Ausbildung einer Bursa copulatrix in die Diskussion einzubringen.

Neben dem als Instrument der Merkmalsbewertung allgemein anerkannten Außengruppenvergleich kann auch eine Analyse der funktionellen Bedingungen und Korrelationen von Merkmalsausprägungen bei der Bestimmung der Lesrichtung von Bedeutung sein (Berthold 1991). Da der Mündungsbereich der Spermathecae der Ort der Spermaaufnahme ist, ist im folgenden auch der Modus des Spermatransfer, also das Paarungssystem von Arten zu berücksichtigen.

Während für das Grundmuster der Diptera sicher die Bildung von Spermatophoren postuliert werden kann, ist offen, ob auf der weiblichen Seite die Gänge der drei Spermathecae getrennt voneinander direkt im Dach der Genitalkammer münden oder ob ihnen Bursa/unpaarer Ductus vorgeschaltet sind.

Bei der Suche nach Korrelationen zwischen dem Modus des Spermatransfer auf der männlichen Seite und der Mündung der Spermathecae findet sich ein bestimmtes, eindeutiges Muster. Während bei Arten, die Spermatophoren bilden, immer eine Bursa copulatrix (Bibionidae) oder ein unpaarer Endabschnitt (Ceratopogonidae, Simuliidae) vorliegt, wird bei Formen mit vollständig getrennten Mündungen der Spermathecae das Sperma immer in freier Form übertragen (Trichoceridae, Neumann 1958; Blepharoceridae, Downes 1968; einige Mycetophilidae). Es sind darüberhinaus aber auch Fälle bekannt, in denen der Transfer (nachweislich) freien Spermas mit Bursa copulatrix (Tipulidae, Neumann 1958) oder unpaarem Endabschnitt der Spermathecae (Sciaridae) korreliert ist.

Der ursprüngliche Modus des Spermatransfer (Spermatophore) kommt also nie bei Formen mit vollständig getrennten und offenen Mündungen der Samenkapseln vor, während der mehrfach unabhängig evolvierte und damit abgeleitete Transfer freien Spermas sowohl bei Arten mit Bursa/unpaarem Ductus als auch bei solchen mit vollständig offenen Mündungen vorkommt. Aus dieser Korrelation läßt sich schließen, daß die Ausbildung einer bursaähnlichen Struktur als ursprünglicher Merkmalszustand zu bewerten ist und damit zum Grundmuster der Diptera gehört. Diese Argumentation bei der Bewertung funktionell zusammengehörender Elemente kann als schlüssig angesehen werden, wird im vorliegenden Fall aber durch den unbefriedigenden Kenntnisstand abgeschwächt. Für die Diptera ist nur in seltenen Fällen der Modus des Spermatransfer **direkt** nachgewiesen: es überwiegen die indirekt aus der Morphologie des männlichen Begattungsorgans gezogenen Rückschlüsse. So ist es nicht auszuschließen, daß es Arten gibt, bei denen die Bildung einer Spermatophore mit der offenen Mündung der Spermathecae korreliert ist; das würde die oben dargelegte Argumentation und die damit verbundene Hypothese falsifizieren.

Dennoch ist es beim derzeitigen Kenntnisstand möglich, eine begründete Entscheidung bezüglich der Merkmalsausprägung für das Grundmuster der Diptera zu treffen, gestützt auf eine Vielzahl von Indizien. Die (a) weite Verbreitung einer bursaähnlichen

Struktur innerhalb der Diptera zusammen mit der Korrelation von Spermatophore und Bursa und (b) der Tatsache, daß es in der weiteren Außengruppe bei den Siphonaptera das Vorhandensein von zwei Spermathecae immer mit der Ausbildung einer Bursa copulatrix verbunden ist, machen wahrscheinlich, daß es sich hierbei um ein Grundmuster-Merkmal der Diptera handelt. Innerhalb dieses Taxon ist der Besitz einer bursaähnlichen Struktur als Symplesiomorphie zu bewerten (die sich auch noch im Grundmuster der Bibionomorpha findet). Die offene Mündung der Spermathecae direkt im Dach der Genitalkammer ist dagegen ein apomorpher Merkmalszustand, der erst innerhalb der Bibionomorpha durch Reduktion der Bursa evolviert worden ist.

Die paarige **akzessorische Drüse** mündet bei allen untersuchten Arten der Bibionomorpha unpaar im Dach der Genitalkammer. Da dies auch für die meisten der daraufhin untersuchten Diptera (nematocere Dipteren: Seather 1977; Chironomidae, Anisopodidae und Mycetophilidae: Abul-Nasr 1950; Asilidae, Reichardt 1929) und in der weiteren Außengruppe für das Grundmuster der Mecoptera (Mickoleit 1976) gilt, kann diese Merkmalsausprägung als plesiomorphes Grundmuster-Merkmal der Diptera aufgefaßt werden. Sie ist unverändert als Symplesiomorphie in das Grundmuster der Bibionomorpha übernommen worden.

Der unpaare Endabschnitt des **Oviduct** (Oviductus communis) mündet bei allen untersuchten Bibionomorpha cranial in die Genitalkammer. Dies ist sicher eine Symplesiomorphie, übernommen mindestens aus dem Grundmuster der Antliophora (Mecoptera: Mickoleit 1976; Siphonaptera: Matsuda 1976: 371). Unverständlich ist daher die Angabe Hennigs (1973: 230, übernommen von McAlpine 1981: 38), der primäre Gonoporus liege in der dorsalen Wand der Genitalkammer. Falls es wirklich Dipteren gibt, bei denen der Oviduct im Dach der Genitalkammer mündet, ist dies als sekundäre Erscheinung innerhalb der Diptera zu werten. Sicher ist, daß im Grundmuster der Bibionomorpha der Oviductus communis cranial in die Genitalkammer mündet.

Zusammenfassung: Die weiblichen Terminalia im Grundmuster der Bibionomorpha
— die Terga der Segmente VIII, IX und X sind vorhanden (Symplesiomorphie);
— das Gonocoxosternit VIII ist paarig (Symplesiomorphie) und überragt caudad das 8. Segment (Symplesiomorphie); sein Ende markiert das unpaare Gonotrema (Symplesiomorphie);
— die Postgenitalplatte, die mit dem Tergum X in Verbindung steht und bis unter die Cerci reicht, ist ausgebildet (Symplesiomorphie);
— die Cerci sind zweigliedrig (Symplesiomorphie);
— im Dach der Genitalkammer befindet sich ein gabelförmiges Sklerit, die Genitalfurca (Symplesiomorphie);
— es sind drei Spermathecae vorhanden (Symplesiomorphie);
— die Gänge der Spermathecae vereinigen sich zu einem unpaaren Endabschnitt (Symplesiomorphie), der im Dach der Genitalkammer mündet (Symplesiomorphie);
— die paarige akzessorischen Drüse mündet unpaar im Dach der Genitalkammer (Symplesiomorphie), der Oviductus communis mündet cranial in das Lumen der Genitalkammer (Symplesiomorphie).

Thorax und Extremitäten

1. Thorakale Sklerite

Ein detaillierte Untersuchung des thorakalen Skeletts in Zusammenhang mit seiner Muskulatur steht für die Bibionomorpha noch aus. Aus diesem Grund beschränkt sich die folgende Rekonstruktion des Grundmusters auf einige wenige auffällige Sklerite, die für die Darstellung der verwandtschaftlichen Beziehungen von Bedeutung sind.

Der für die Rekonstruktion des Grundmusters nötige Außengruppenvergleich ist gerade hinsichtlich thorakaler Merkmale wenig ergiebig, da der Thorax der Dipteren durch die Reduktion des metathorakalen Flügelpaares eine tiefgreifende Umgestaltung erfahren hat und bereits im Grundmuster stark abgeleitete Züge trägt. Somit stützt sich die Merkmalsbewertung weitgehend auf einen Vergleich der Merkmalsausprägungen innerhalb der Diptera.

Im Grundmuster der Bibionomorpha enthält der Prothorax noch Ante-und Postpronotum, denn beide Sklerite kommen zusammen sowohl innerhalb der Bibioniformia (Hesperinidae: Crampton 1925) als auch der Mycetophiliformia (Sciaridae, viele Mycetophilidae: Shaw & Shaw 1951) vor. Diese Merkmalsausprägung ist als Symplesiomorphie zu bewerten, da sie aus dem Grundmuster der Diptera übernommen worden ist (Crampton 1942).

Das Episternum des Mesothorax ist durch eine Naht asymmetrisch in das kleinere An- und das größere Katepisternum geteilt. Diese Asymmetrie ist innerhalb der Mycetophiliformia weit verbreitet, lediglich bei den Arten der Mycetophilinae (Mycetophilidae) sind beide Anteile etwa gleich groß (Shaw 1948). Da bei den Bibioniformia das Episternum ebenfalls asymmetrisch geteilt ist (Hesperinidae, Bibionidae: Crampton 1925), ist anzunehmen, daß die Merkmalsausprägung bei den Mycetophilinae sekundärer Natur ist. Begründen ließe sich diese Festlegung der Lesrichtung mit der starken Abflachung des ursprünglich hoch gewölbten Thorax, denn die Symmetrie von An- und Katepisternum ist bei den Mycetophilinae mit dieser Stauchung des Thorax korreliert.

In der engeren Außengruppe (Diptera) ist die Ausbildung von zwei annähernd gleichgroßen Teilen des Episternum weit verbreitet (Trichoceridae, Axymyiidae, Psychodidae, Blephariceridae: Crampton 1925; Tipulidae, Brachycera: Hennig 1973: 177), aber auch eine asymmetrische Teilung des Sklerits kommt vor (Psychodidae, Anisopodidae, Culicomorpha: Crampton 1925).

Der weitere Außengruppenvergleich kann bei der Merkmalsbewertung nicht helfen, da sowohl bei den Mecoptera als auch den Siphonaptera im Grundmuster das Mesepisternum vermutlich noch ungeteilt ist (Snodgrass 1935: 179; Hopkins & Rothschild 1953). So läßt sich lediglich aus der Verteilung der beiden verschiedenen Merkmalsausprägungen innerhalb der Diptera und der Bibionomorpha schließen, daß die asymmetrische Teilung des Mesepisternum bereits ein Grundmuster-Merkmal der Bibionomorpha ist. Die Bewertung dieser Merkmalsausprägung ist nur dann möglich, wenn die Schwestergruppe der Bibionomorpha bekannt ist. Es ist festzuhalten, daß bei beiden potentiellen Schwestergruppen der Bibionomorpha, Blephariceridae und Brachycera (Colless & McAlpine 1970), das Episternum des Mesothorax aus zwei annähernd gleichgroßen Teilen besteht.

Das Epimerum des Mesothorax ist bei den Mycetophiliformia basal deutlich eingeengt, während es bei den Vertretern der Bibioniformia breit die Basis der Coxa erreicht

(Crampton 1925). Da bei der Mehrzahl der Dipteren das Epimerum sich basal nicht verjüngt (Crampton 1925), kann angenommen werden, daß bei den Bibioniformia diese ursprüngliche Merkmalsausprägung aus dem Grundmuster der Bibionomorpha übernommen worden ist. Die Abänderung dieses Merkmals in Form der basalen Verengung erfolgte erst innerhalb des Taxon in der Stammlinie der Mycetophiliformia und ist dann als abgeleitet zu bewerten.

Das endoskletale Postphragma ist bei den meisten Dipteren groß ausgebildet und ragt bis in das erste abdominale Segment hinein (Colless & McAlpine 1970). Dies gilt auch für die Bibioniformia und einen Teil der Mycetophiloidea (Cecidomyiidae, Sciaridae, Diadocidiidae). Bei den Mycetophilidae aber ist das Postphragma sehr viel kürzer und verläuft nur bis unter das Mediotergit. Diese Merkmalsausprägung ist korreliert mit einer Verschmälerung der Abdomenbasis wie es auch innerhalb der Diptera bei anderen Taxa zu finden ist (z. B. Tipulidae). Es kann kaum ein Zweifel daran bestehen, daß die große Ausdehnung des Postphragma ein Grundmuster-Merkmal der Bibionomorpha ist. Eine Verkürzung des Phragmas wurde erst innerhalb der Bibionomorpha bei den Mycetophilidae erreicht und ist gegenüber dem Grundmuster als abgeleitet zu bewerten.

2. Coxae

Die Coxen, die als Basis der Extremitäten zwischen diesen und dem Thorax vermitteln, sind innerhalb der Bibionomorpha sehr verschieden geformt. Während sie bei den Bibioniformia (Pachyneuroidea: Krivosheina & Mamayev 1970, Wood 1981; Hesperinidae, Bibionidae: Crampton 1925) kurz und schmal sind, sind sie bei den meisten Mycetophiliformia (Sciaridae, Diadocidiidae und Mycetophilidae) auffallend lang und kräftig gebaut (Shaw & Shaw 1951). Um die Ausprägung der Coxen im Grundmuster der Bibionomorpha beurteilen zu können, ist ein Außengruppenvergleich notwendig.

In der engeren Außengruppe (Diptera) sind die Coxen im Verhältnis zur Höhe des Thorax kürzer ausgebildet als bei den Mycetophiliformia (Crampton 1925, 1942). Anders sieht es dagegen in der weiteren Außengruppe bei den Mecoptera und Siphonaptera aus. Die Basis der Extremitäten ist bei den Siphonaptera kräftig entwickelt, was mit dem sicher zum Grundmuster des Taxon gehörenden Sprungvermögen (Hennig 1969: 294) zusammenhängt. Die Ausdehnung der Coxen im Grundmuster der Mecoptera ist nicht bekannt, doch ist verschiedenen Abbildungen zu entnehmen, daß zumindest bei einigen Vertretern (Panorpidae) die Hüften relativ lang sind (z. B. Weber 1974: 396; Snodgrass 1935: 179).

Der Vergleich in der weiteren Außengruppe deutet darauf hin, daß bereits die letzte Stammart der Diptera verlängerte Coxen besessen haben könnte. Diese Annahme steht aber im Widerspruch zu der weiten Verbreitung kurzer Coxen innerhalb der Diptera. Denn in diesem Fall müßten die Coxen in ihrer Länge innerhalb der Diptera vielfach unabhängig reduziert worden sein und wären innerhalb der Mycetophiliformia lediglich bei Sciaridae, Diadocidiidae und Mycetophilidae in ihrem ursprünglichen Ausmaß erhalten geblieben. Nimmt man dagegen für das Grundmuster der Diptera den Besitz kurzer Coxen an, so sind nur einige wenige Fälle einer Verlängerung dieses Extremitätenglieds zu postulieren. Denn solange die funktionelle Bedeutung der Coxen-Länge nicht klar ist, bleibt man bei der Merkmalsbewertung auf eine ausschließliche Wahrscheinlichkeits-Entscheidung angewiesen.

Mani (1952) erklärt zwar die starke Verlängerung der Coxen bei den Mycetophilidae damit, daß diese sich aus einer Puppenhaut, die nicht im Boden verankert ist, befreien

müßten. Diese Erklärung ist aber nicht schlüssig, da viele Mycetophilidae ein stabiles Puppengespinst bauen (Plachter 1979a,c) und weil die Imagines von Arten, die sich in festem Substrat verpuppen (*Ditomyia* in Konsolenpilzen, *Symmerus* im Holz von Laubbäumen), ebenfalls extrem lange Coxen aufweisen.

Aufgrund einer Wahrscheinlichkeitsentscheidung wird hier angenommen, daß die letzte Stammart der Bibionomorpha kurze Coxen besessen hat und daß diese Merkmalsausprägung aus dem Grundmuster der Diptera übernommen worden ist. Eine Verlängerung der Coxen erfolgte erst innerhalb der Mycetophiliformia.

3. Tibialorgan

Ein drüsig differenziertes Tibialorgan im subapikalen Bereich der Vordertibia findet sich innerhalb der Bibionomorpha nur bei Sciaridae, Diadocidiidae und Mycetophilidae. Obwohl das Tibialorgan innerhalb der Mycetophiloidea in verschiedenen Merkmalsausprägungen vorliegt, kann an der Homologie dieser Strukturen nicht gezweifelt werden. Identische Lage, Ausbildung in beiden Geschlechtern und die spezielle Ausprägung in Verbindung mit einer Drüsenplatte belegen diese Annahme.

Für die Bibioniformia gibt es keinen Hinweis auf die Existenz einer vergleichbaren Struktur. Die Frage, ob ein Tibialorgan dennoch zum Grundmuster der Bibionomorpha gehört und bei den Bibioniformia lediglich restlos reduziert ist, läßt sich mit Hilfe des Außengruppen-Vergleichs eindeutig beantworten. Derartige Differenzierungen der Tibiae — verbunden mit einer Drüse — sind innerhalb der Diptera nur noch von verschiedenen Brachycera bekannt. Nach Hennig (1949) ist ein Tibialorgan bei einigen Sepsidae im männlichen Geschlecht zu finden; diese Differenzierung, als Osmoterium bezeichnet, befindet sich aber auf der Tibia des 3. Beinpaares.

Desweiteren sind Tibialorgane bei Dolichopodidae und Hybotidae bekannt (Hennig 1973: 201). Das bei den Hybotidae auftretende Tibialorgan wird von Tuomikoski (1966) als Autapomorphie dieser Gruppe angesehen. Hier ist die Mündung eines Drüsengangs auf der Vordertibia immer durch ein dichtes Borstenfeld markiert. Eine Abbildung dazu findet sich in einer früheren Arbeit (Tuomikoski 1937); diese zeigt, daß das Tibialorgan im basalen Bereich der Tibia lokalisiert ist.

Das Tibialorgan der Dolichopodidae scheint nur von *Dolichopus* bekannt zu sein. Die Untersuchung von Kazjakina (1966) zeigt, daß es sich wiederum — wie bei den Sepsidae — um eine Differenzierung der Hintertibien handelt. Die dazugehörigen Drüsenzellen bilden Kanälchen aus, die einzeln an der Basis von Borsten ausmünden.

Die Tibialorgane der verschiedenen Brachycera unterscheiden sich wesentlich von dem der Mycetophiloidea. Während dieses immer im subapikalen Bereich der Vordertibia lokalisiert, in beiden Geschlechtern ausgeprägt und mit einer einfachen Drüsenplatte verbunden ist, liegt das Tibialorgan der Sepsidae auf der Hintertibia und ist darüberhinaus auch noch sexualdimorph ausgebildet, da es nur bei den Männchen vorkommt. Das Tibialorgan der Hybotidae, das vermutlich erst innerhalb der Empidoidea evolviert worden ist, liegt zwar auf der Vordertibia, dort aber im basalen Bereich; auch ist die Drüse nicht als einfache Drüsenplatte ausgebildet, sondern tubulär strukturiert. Auch das Tibialorgan, das innerhalb der Dolichopodidae bei *Dolichopus* zu finden ist, unterscheidet sich gravierend von dem der Mycetophiloidea: es liegt auf der Hintertibia und die Drüsenzellen bilden direkt einzelne Kanälchen aus.

Die Verbreitung eines Tibialorgans innerhalb der Diptera und die Unterschiede in der Ausprägung, die Lage, cuticulare Differenzierung und Drüsentyp betreffen, machen

wahrscheinlich, daß das Tibialorgan der Mycetophiloidea kein Homologon innerhalb der übrigen Dipteren hat; die Tibialorgane bei verschiedenen Brachycera sind unabhängig davon entstanden.

Daher kann angenommen werden, daß ein Tibialorgan dieser Ausprägung (Grube mit Drüsenplatte) nicht zum Grundmuster der Bibionomorpha gehört und erst innerhalb des Taxon evolviert worden ist; es handelt sich um einen innerhalb der Mycetophiliformia abgeleiteten Merkmalszustand.

4. Tarsus

Am fünfgliedrigen Tarsus der Bibionomorpha ist nur die Ausprägung der Pulvillen von besonderem Interesse. Pulvillen sind paarige, in der Regel lappenförmige Haftstrukturen des Praetarsus mit ventralem Trichombesatz (Röder 1986). Sie sind sehr wahrscheinlich erst innerhalb der Diptera evolviert worden (Hennig 1973: 199). Sicher monophyletische Taxa, deren Vertreter wohlentwickelte Pulvillen besitzen, sind die Culicomorpha und die Brachycera. Innerhalb der Bibionomorpha weisen sich die Bibioniformia ebenfalls durch den Besitz solcher Haftlappen aus (Krivosheina & Mamayev 1970, Hardy 1981, Wood 1981). Dagegen sind bei allen Mycetophiliformia die Pulvillen klein und fehlen häufig ganz. Ähnliche Verhältnisse liegen auch bei den Anisopodidae und Scatopsoidea vor. Vollständig fehlen Pulvilli bei Tipulidae, Trichoceridae, Blephariceridae und den Psychodomorpha. Diese Merkmalsverteilung läßt verschiedene Interpretationen mit folgenden Konsequenzen zu:

a) Pulvillen sind innerhalb der Diptera nur einmal entstanden. Dies entspricht der Vorstellung Hennigs, der den Besitz von Pulvilli als mögliche Synapomorphie von Culicomorpha, Bibionomorpha und Brachycera in Erwägung zieht (1968). Formen, die keine Pulvillen haben, könnten danach sowohl den ursprünglichen als auch einen abgeleiteten Zustand (durch vollständige Reduktion) repräsentieren. Kleinere, aber deutlich ausgebildete Haftlappen können dann nur als Reduktionserscheinungen gedeutet werden. Bei dieser Interpretation gehört ein Paar Pulvillen sicher zum Grundmuster der Bibionomorpha, es ist dann innerhalb des Taxon bei den Mycetophiliformia reduziert worden.

b) Pulvillen sind mehrfach konvergent innerhalb der Diptera entstanden. Sind sie nur schwach ausgeprägt, könnte dies neben Reduktion auch als Neuentstehung (noch nicht vollständig ausgeprägt) interpretiert werden (Röder 1986). In diesem Fall wäre es denkbar, daß Pulvillen nicht zum Grundmuster der Bibionomorpha gehören, sondern erst zu dem der Bibioniformia.

c) Die Ausprägung von Pulvillen ist ein autapomorphes Grundmuster-Merkmal der Diptera. Der Besitz lediglich kleiner Pulvillen oder ihr völliger Mangel sind immer auf Reduktionserscheinungen zurückzuführen.

Für die letztgenannte Hypothese lassen sich keine Indizien anführen; es spricht nichts dafür, daß bereits die letzte Stammart der Tipulidae oder Trichoceridae Pulvillen besessen haben könnte. Das gleiche gilt auch für die Taxa, die als Psychodomorpha zusammengefaßt werden.

Die Annahme einer mehrmaligen, konvergenten Entstehung von Pulvillen steht zwar in Einklang mit dem Verteilungsmuster der Merkmalsausprägungen und bietet auch den — scheinbaren — Vorteil, daß weniger Reduktionen postuliert werden müssen. Allerdings erscheint die mehrmalige Neuentstehung von Pulvilli-artigen Strukturen relativ unwahrscheinlich. Ein Blick auf den Rest der Pterygota zeigt, daß solche Haftlappen

äußerst selten evolviert worden sind (z. B. Homoptera mit „Pseudopulvillen" (Röder 1986)). Dagegen lassen sich Reduktionen von Pulvilli häufig mit der Lebensweise (Remmert 1960) und einer Reduktion von Körpergröße (und Körpergewicht!) korrelieren.

Aus diesen Gründen erscheint die erstgenannte Hypothese am wahrscheinlichsten. Der Besitz von Pulvillen ist ein (symplesiomorphes) Grundmuster-Merkmal der Bibionomorpha, Arten mit reduzierten Pulvilli (alle Mycetophiliformia) sind bezüglich dieses Merkmals als abgeleitet zu betrachten.

Zusammenfassung: Thorax und Extremitäten im Grundmuster der Bibionomorpha
— das Episternum des Mesothorax ist asymmetrisch geteilt (Autapomorphie);
— das Epimerum des Mesothorax ist basal nicht eingeengt, sondern erreicht breit die Basis des Thorax (Symplesiomorphie);
— das Postphragma ragt bis in das 1. abdominale Segment (Symplesiomorphie);
— die Coxen sind in Relation zum Thorax nicht auffallend verlängert (Symplesiomorphie);
— am vorderen Beinpaar ist kein Tibialorgan ausgebildet (Symplesiomorphie);
— am Tarsus sind die Pulvillen wohlentwickelt (Symplesiomorphie).

Flügelgeäder

Die umfangreiche Arbeit Hennigs über Flügelgeäder und System der Diptera (1954) zeigt deutlich, daß die Bewertung von Merkmalen aus diesem Komplex in starkem Maße von Vorstellungen über die verwandtschaftlichen Beziehungen abhängig ist. Das hängt damit zusammen, daß es sich bei den betreffenden Merkmalsausprägungen meist um einfache Reduktionen von Flügeladern handelt, die stark konvergenzverdächtig sind. Aus diesem Grunde sollte der Ausprägung des Flügelgeäders bei der Rekonstruktion verwandtschaftlicher Beziehungen keine entscheidende Bedeutung beigemessen werden.

Für die Rekonstruktion des Grundmusters der Bibionomorpha hinsichtlich der Ausprägung des Flügelgeäders ist von Bedeutung, daß die Pachyneuroidea ein relativ ursprüngliches Adermuster aufweisen. So ist das Vorhandensein der Diskalzelle bei *Cramptonomyia, Haruka* und *Pergratospes* (Wood 1981) ein Merkmal, das aus dem Grundmuster der Diptera (Hennig 1973: 190) übernommen wurde und damit auch Grundmuster-Merkmal der Bibionomorpha ist. Innerhalb der Bibionomorpha muß die Diskalzelle dann vielfach reduziert worden sein, denn sie fehlt bei *Pachyneura*, Bibionoidea und Mycetophiliformia (Hennig 1954).

Ähnliches gilt für den 3. Ast der Media (M3), der ebenfalls nur noch bei den oben genannten drei Arten der Pachyneuroidea vorkommt, aber eindeutig Grundmuster-Merkmal der Diptera ist (Hennig 1973: 190).

Der Radialsektor (R) bildet sowohl bei den Bibioniformia als auch Mycetophiliformia nur drei Äste aus (Hennig 1954); diese Merkmalsausprägung gehört damit sicher zum Grundmuster der Bibionomorpha.

Die Randader (Costa), die im Grundmuster der Diptera den ganzen Flügel umzieht (Hennig 1973: 190), reicht bei den meisten Arten sowohl der Bibioniformia als auch der Mycetophiliformia nicht über die Mündung von R5 in den Flügelrand hinaus (Hennig 1954). Die bei Cecidomyiidae vorkommende große Ausdehnung der Costa um den gesamten Flügelrand (Gagné 1981) ist wahrscheinlich sekundärer Natur. Dieser scheinbar ursprüngliche Merkmalszustand kommt bei Formen vor, die die Längsadern des Flügels weitgehend reduziert haben (Mamayev & Krivosheina 1965); die Verlängerung

der Costa könnte daher in funktionellem Zusammenhang mit der Stabilisierung der Flügelfläche stehen. Die Alternative, daß die ursprüngliche Länge der Costa innerhalb der Bibionomorpha nur bei Gallmücken mit extrem reduziertem Flügelgeäder erhalten geblieben ist, ist sehr unwahrscheinlich.

Aus dieser Zusammenstellung der Ausprägung verschiedener Flügeladern geht hervor, daß die letzte Stammart der Bibionomorpha ein Flügelgeäder besessen haben dürfte, dem rezent das von *Cramptonomyia spenceri* (Krivosheina & Mamayev 1970, Abb.4) nahekommt. Innerhalb der Bibionomorpha ist es dann vielfach zu Reduktionen gekommen, deren Bewertung erst anhand des Verwandtschaftsdiagramms möglich sein wird.

Imaginale Mundwerkzeuge

Die Imagines sowohl der Bibioniformia als auch der Mycetophiliformia zeichnen sich durch das Fehlen der Mandibeln in beiden Geschlechtern aus (Hennig 1973: 30). Diese Merkmalsausprägung, die zum Grundmuster der Bibionomorpha gehört, ist als abgeleitet zu bewerten, da die letzte Stammart der Diptera in beiden Geschlechtern noch Mandibeln besessen hat (Hennig 1973: 153). Dagegen sind die anderen Teile des Rüssels im Grundmuster der Bibionomorpha erhalten: Labrum, Maxille mit den fünfgliedrigen Maxillarpalpen, Labium und Hypopharynx (Frey 1913).

Merkmale der präimaginalen Stadien

1. Larvale Stigmenausstattung

Innerhalb der Bibioniformia besitzen die Larven der Hesperinidae und Bibionidae zehn Paar Stigmen (Hardy 1981; holopneustisches Tracheensystem, Terminologie nach Hennig 1973: 120), die der Pachyneuroidea nur neun Paare (Wood 1981), wobei das des Metathorax fehlt (peripneustisches Tracheensystem); Krivosheina & Mamayev weisen aber darauf hin (1970), daß bei *Pergratospes* ein weitgehend reduziertes Stigmenpaar am metathorakalen Segment vorhanden ist. Damit ist wahrscheinlich, daß ein holopneustisches Tracheensystem zum Grundmuster der Bibioniformia gehört. Ob dies auch für das Grundmuster der Bibionomorpha gilt, sollen im folgenden Innen- und Außengruppenvergleich zeigen.

Am weitesten verbreitet ist bei den Larven der Diptera ein amphipneustisches Tracheensystem (Hennig 1973: 121). Daneben kommen aber in verschiedenen Teiltaxa — wenn auch viel seltener — holo- und peripneustische Larven vor. Der Außengruppen-Vergleich zeigt, daß die Larven der zur Diskussion stehenden potentiellen Schwestergruppen der Diptera (Mecoptera, Siphonaptera) in den Larvenstadien durch den Besitz aller oder fast aller Stigmenpaare gekennzeichnet sind; die Präimaginalstadien der Siphonaptera sind holopneustisch (Hinton 1947), die der Mecoptera im Grundmuster mindestens peripneustisch (Kaltenbach 1978: 83).

Somit kann für das Grundmuster der Diptera mit genügender Wahrscheinlichkeit ein holopneustisches Tracheensystem angenommen werden. Diese Merkmalsausprägung ist unverändert in das Grundmuster der Bibionomorpha übernommen worden.

2. Larvale Mandibel

Die Larven sowohl der Bibioniformia (Schremmer 1956, Krivosheina & Mamayev 1970, Wood 1981) als auch der Mycetophiliformia (Plachter 1979b) zeichnen sich durch ein-

gliedrige, horizontal bewegliche Beißmandibeln aus. Abweichungen von dieser Merkmalsausprägung gibt es nur bei den Cecidomyiidae, deren Mandibeln zu Stiletten umgewandelt sind (Hennig 1952). Es kann kein Zweifel daran bestehen, daß der Besitz einer einteiligen, horizontal beweglichen Mandibel ein Grundmuster-Merkmal der Bibionomorpha ist.

Der für die Bewertung dieser Merkmalsausprägung durchgeführte Außengruppen-Vergleich zeigt, daß bei fast allen übrigen nematoceren Diptera und Brachycera eine schräg oder gänzlich vertikal bewegliche Mandibel, die häufig auch zweigeteilt ist, vorkommt (Hennig 1948, 1952; Bischoff 1922; Anthon 1943; Schremmer 1956). Dagegen findet sich eine einteilige, horizontal bewegliche Mandibel außerhalb der Bibionomorpha nur noch innerhalb der Tipulidae (Alexander & Byers 1981). Damit stellt sich die Frage, wie die Mandibel der letzten Stammart der Diptera ausgesehen hat und in welcher Ebene sie bewegt worden ist.

Über die Bewertung der zweiteiligen Mandibel hat es einige Verwirrung gegeben. Anthon (1943) hat die Zweiteilung auf die ursprüngliche Gliederung der Arthropoden-Extremität zurückgeführt und sie damit — durchaus folgerichtig — auch als ursprünglich für die Diptera angesehen. Demgegenüber wies Snodgrass (1950) darauf hin, daß die scheinbare Gliederung vermutlich durch partielle Desklerotisierung entstanden ist und nichts mit der ursprünglichen Gliederung einer Arthropoden-Extremität zu tun hat. Denn für die Hexapoda ist der Besitz einer eingliedrigen Mandibel als ursprünglich anzusehen, die zweiteilige Mandibel vieler Dipteren-Larven wäre somit — in Bezug auf das Grundmuster der Hexapoda — ein abgeleiteter Zustand.

Schremmer (1956) dagegen hält die zweiteilige Mandibel dennoch für den ursprünglichen Zustand innerhalb der Diptera. In die Termini der Phylogenetischen Systematik übersetzt bedeutet dies, daß bereits die letzte Stammart der Diptera zweigeteilte Mandibeln besessen hat und daß diese Merkmalsausprägung als Autapomorphie der Diptera bewertet werden kann. Dieser Auffassung hat sich wohl auch Hennig (1973: 110) — wenn auch nicht in aller Deutlichkeit — angeschlossen. Dies bedeutet aber auch, daß eingliedrige, horizontal bewegliche Beißmandibeln innerhalb der Diptera als abgeleitet bewertet werden müßten. Allerdings ist an dieser Stelle nochmals darauf hinzuweisen, daß diese Schlußfolgerung nicht in Einklang mit den Befunden des weiteren Außengruppenvergleichs steht. Denn es ist wahrscheinlich, daß die larvalen Mandibeln sowohl im Grundmuster der Siphonaptera (Kaestner 1973: 802) als auch in dem der Mecoptera (Kaltenbach 1978) horizontal beweglich sind.

Eine partielle Desklerotisierung und Zweiteilung der Mandibeln ist nur dann möglich, wenn diese beim Nahrungserwerb keine Festhaltefunktion mehr auszuüben haben, sondern eher dem Sammeln („Zusammenfegen") von lockerem Substrat dienen. Darauf weist auch die Korrelation dieser Merkmalsausprägung mit einer starken Schrägstellung der Mandibeln hin (Schremmer 1951). Aber umgekehrt sind nicht alle schräggestellten Mandibeln gleichzeitig zweigeteilt. Es könnte hilfreich sein, diese beiden Ausprägungen in den weiteren Ausführungen getrennt zu betrachten.

Es ist auffallend, daß innerhalb der Diptera horizontal bewegliche Beißmandibeln nur bei Bibioniformia, Mycetophiliformia und einigen Tipulidae auftreten. Die Hypothese, daß diese Merkmalsausprägung noch den ursprünglichen Zustand repräsentiert, führt zu der Annahme mehrfacher, konvergenter Verschiebung der Bewegungsebene der Mandibeln innerhalb der Diptera, denn ein Schwestergruppen-Verhältnis zwischen bei-

den Taxa ist sehr unwahrscheinlich und kann nicht durch weitere Argumente belegt werden. Bei den sicher monophyletischen Tipulidae, bei denen beide Typen vorkommen, scheint die Stellung der Mandibeln mit der Art des Nahrungssubstrates der Larven korreliert zu sein. Die häufig abgebildete *Tanyptera* (Hennig 1948, Schremmer 1951) mit kräftigen Beißmandibeln gehört zu den **holz**bewohnenden (hartes Nahrungssubstrat) Ctenophorinae. Ähnliches könnte auch für die ebenfalls in der Horizontalen beweglichen spitzen Raubmandibeln (Festhaltefunktion der Mandibeln) einiger Tipulidae angenommen werden. Zumindest also für die Tipulidae kann mit einer Rückdrehung der Mandibeln in die für Hexapoda typische Lage gerechnet werden, zumal auch zum Grundmuster ihrer mutmaßlichen Schwestergruppe, der Trichoceridae (?), schräg ventrad gerichtete Mandibeln gehören (Hennig 1948).

Wenn die Beißmandibeln der Bibioniformia und Mycetophiliformia demgegenüber den (immer noch) ursprünglichen Zustand repräsentieren, könnte ein Schwestergruppen-Verhältnis zwischen diesen und allen übrigen Diptera (einschließlich der Brachycera) angenommen werden. Diese Hypothese läßt sich aber mit keinem weiteren Merkmal stützen und gerät darüberhinaus auch noch in Konflikt mit anderen, ebenfalls begründeten Vorstellungen, die auf Merkmalsausprägungen der Flügelbasis (Hennig 1968) und des Praetarsus (Hennig 1968, 1973: 22; Röder 1986) basieren.

Gegen die Vorstellung, die Drehung der Mandibel bis zur vertikalen Stellung ist innerhalb der Diptera mehrfach unabhängig entstanden, spricht nur ihr geringer Wahrscheinlichkeitsgrad. Gegenargumente, die sich auf funktionelle und morphologische Bedingungen stützen könnten, lassen sich nicht anführen.

Nimmt man aber für das Grundmuster der Diptera den Besitz eines schräg oder vertikal beweglichen Mandibelpaares an, so ist die horizontal bewegliche Beißmandibel dann mindestens zweimal unabhängig innerhalb dieses Taxon entstanden (Bibionomorpha, Tipulidae). Korreliert ist diese Stellung mit einer rein terrestrischen Lebensweise, die Rohdendorf (1974: 62) als typisch für die meisten Bibionomorpha ansieht, verbunden mit relativ hartem Nahrungssubstrat. Demgegenüber hat die letzte Stammart der Diptera die Larvalentwicklung vermutlich in einem semiaquatischen Milieu verbracht (Hinton 1947).

Der Besitz schräg ventrad gerichteter Mandibeln ist als Praedisposition für die Entstehung von partiell desklerotisierten, zweiteiligen Mandibeln zu betrachten. Der Besitz derartiger Mandibeln ist korreliert mit dem Vorkommen der Larven in relativ flüssigen Substraten, wobei Nahrungspartikel mit den Mandibeln zusammengefegt werden (Schremmer 1951). So ist es nicht unwahrscheinlich, daß diese Form der Mandibel mehrfach unabhängig innerhalb der Diptera evolviert wurde und damit einen abgeleiteten Zustand repräsentiert. Teskey (1981) geht ebenfalls davon aus, daß zumindest bei den Brachycera die Zweiteilung unabhängig entstanden ist.

Zusammenfassend kann gesagt werden, daß der Besitz einer eingliedrigen, in der Horizontalen beweglichen Mandibel ohne jeden Zweifel ein Grundmuster-Merkmal der Bibionomorpha ist. Das Vorkommen dieser Merkmalsausprägung bei fast allen Vertretern des Taxon läßt keinen anderen Schluß zu. Aber die Bewertung des Merkmals kann nicht so eindeutig erfolgen. Beim derzeitigen Kenntnisstand scheint es am wahrscheinlichsten, daß die letzte Stammart der Diptera schräg oder vertikal gestellte Mandibeln besessen hat; innerhalb des Taxon ist es dann zweimal unabhängig (Tipulidae, Bibionomorpha) zu einer Rückdrehung der Mandibeln in die horizontale Bewegungsebene

gekommen. Damit ist der Besitz solcher Mandibeln für das Grundmuster der Bibiono-morpha als abgeleitet zu bewerten.

3. Larvale Antenne

Bei den meisten Bibionomorpha ist die larvale Antenne bis auf ein Glied scheibenför-mig verkürzt (Krivosheina & Mamayev 1970, Plachter 1979b, Hardy 1981, Wood 1981). Lediglich innerhalb der Mycetophiliformia besitzen Larven der Cecidomyiidae (Mama-yev & Krivosheina 1965) und Mycetophilidae (Ditomyiinae, Bolitophilinae, Plachter 1979b) eine spitzkonische, dreigliedrige Antenne. Da im Grundmuster der Diptera die larvale Antenne aus mehreren (6?) Gliedern besteht (Hennig 1973: 112), kann die drei-gliedrige Antenne als Merkmalsausprägung für das Grundmuster der Bibionomorpha angenommen werden. Dieser Merkmalszustand ist noch in das Grundmuster der Myce-tophiliformia übernommen worden, während in der Stammlinie der Bibioniformia die Reduktion der Antennenglieder weiter fortgeschritten ist. Da die Larven aller bekannter Bibionoidea und Pachyneuroidea eine eingliedrige scheibenförmige Antenne besitzen, ist es wahrscheinlich, daß diese abgeleitete Merkmalsausprägung bereits im Grundmu-ster der Bibioniformia vorhanden ist.

4. Beinscheiden

Die Beinscheiden der Puppen sind innerhalb der Bibionomorpha verschieden ausge-prägt. Während sie bei den Bibioniformia teilweise übereinander liegen (Morris 1921, Hennig 1948), sind sie bei der Mehrzahl der Mycetophiliformia in einer Ebene neben-einander angeordnet (Hennig 1948, Plachter 1979c).

Der Außengruppen-Vergleich zeigt, daß auch innerhalb der übrigen Diptera beide Merkmalsausprägungen auftreten (Hennig 1950). Auch wenn in der Außengruppe weder für die Siphonaptera noch für die Mecoptera die Lage der Beinscheiden im Grundmuster bekannt ist, scheinen in beiden Taxa übereinanderliegende Beinscheiden zu dominieren (Mecoptera, Kaltenbach 1978: 85; Siphonaptera, Séguy 1951: 755). Mit dieser Merkmalsverteilung gewinnt die Annahme an Wahrscheinlichkeit, daß auch die letzte Stammart der Diptera im Puppenstadium übereinanderliegende Beinscheiden besessen hat. Diese Merkmalsausprägung ist innerhalb der Diptera vielfach unabhängig abgewandelt worden.

Es ist naheliegend, daß eine Umlagerung der Beinscheiden in Zusammenhang steht mit dem Lokomotionsvermögen der Puppen und/oder dem Substrat, in dem die Verpup-pung erfolgt. Die Lage der Beinscheiden in einer Ebene führt dazu, daß die Ventralseite der Puppe insgesamt flacher und glatter wird.

Eine Korrelation mit dem Lebensraum ist aber nur bei Formen zu erkennen, die in stark strömendem Wasser leben; sowohl bei Blephariceridae als auch Deuterophlebiidae lie-gen die Beinscheiden in einer Ebene nebeneinander.

Die Merkmalsausprägung aus dem Grundmuster der Diptera ist unverändert in das der Bibionomorpha übernommen und erst innerhalb des Taxon bei den Mycetophiliformia abgewandelt worden. Es stellt sich nun die Frage, wie die Merkmalsverteilung innerhalb der Mycetophiliformia zu bewerten ist. Fast alle (bekannten) Puppen haben nebenein-ander liegende Beinscheiden, lediglich einige Mycetophilidae (Macrocerinae, *Apolepht-hisa subincana*, Plachter 1979c) weichen von diesem Schema ab. Es kann nicht ausge-schlossen werden, daß dies zumindest bei *A. subincana* ein sekundärer Zustand ist;

Plachter (1979c) weist in diesem Zusammenhang ausdrücklich auf die kurzen Bein-
scheiden dieser Art hin.

Entweder sind also innerhalb der Mycetophiliformia bei den Puppen die Beinscheiden
mehrfach konvergent in eine Ebene verlagert worden oder aber ein ursprünglich schei-
nender Zustand ist sekundär zweimal unabhängig innerhalb der Mycetophilidae
erreicht worden. Rein numerisch erscheint letzteres am wahrscheinlichsten, so daß für
das Grundmuster der Mycetophiliformia ein Puppenstadium mit in einer Ebene liegen-
den Beinscheiden postuliert werden kann. Dieser Merkmalszustand ist gegenüber dem
Grundmuster der Bibionomorpha abgeleitet.

**Zusammenfassung: Präimaginale Merkmalsausprägungen im Grundmuster der Bibio-
nomorpha**
— die Larven sind holopneustisch (Symplesiomorphie);
— die larvale Mandibel wird horizontal bewegt (Autapomorphie) und ist einteilig (Sym-
plesiomorphie);
— die Larven besitzen eine dreigliedrige Antenne (Symplesiomorphie);
— bei den Puppen liegen die Beinscheiden übereinander (Symplesiomorphie).

Verwandtschaftliche Beziehungen innerhalb der Bibionomorpha (Abb.278-280)

Bevor im Folgenden Taxa der Bibionomorpha als geschlossene Abstammungsgemein-
schaften begründet und Schwestergruppen-Verhältnisse diskutiert werden, wird die
Monophylie der Bibionomorpha (Bibioniformia + Mycetophiliformia) begründet.

Die Bewertung der Grundmuster-Merkmale mit Hilfe des Außengruppenvergleichs hat
gezeigt, daß die meisten Merkmalsausprägungen im Grundmuster der Bibionomorpha
als Symplesiomorphien anzusprechen sind. Es gibt aber einige Merkmale aus verschie-
denen Bereichen (Semaphoronten Imago und Larve, Flügelgeäder, Mundwerkzeuge,
männliches Genitale, Thorax), die apomorphen Charakter aufweisen und daher zur
Begründung der Monophylie des Taxon herangezogen werden können.

(1) Mandibeln der Imagines in beiden Geschlechtern restlos reduziert
Diese Merkmalsausprägung kann ohne Widerspruch als Autapomorphie der Bibiono-
morpha bewertet werden, da die als Schwestergruppe in Frage kommenden Brachycera
und/oder Blephariceridae in ihrem Grundmuster noch gut entwickelte Mandibeln auf-
weisen (Hennig 1973: 22, 39). Es muß aber darauf hingewiesen werden, daß die Mandi-
beln innerhalb der Diptera vielfach unabhängig reduziert worden sind. So besitzen nach
Hennig (1973) z. B. die Imagines der Tipuloidea und Trichoceridae (: 20), der Chirono-
midae (: 29), Anisopodidae und Scatopsoidea (: 30) keine Mandibeln mehr. Aus diesem
Grund ist die Reduktion der imaginalen Mandibeln konvergenzverdächtig, die Begrün-
dung der Bibionomorpha als geschlossene Abstammungsgemeinschaft kann sich nicht
allein auf dieses Argument stützen.

(2) Mandibeln der Larven werden horizontal bewegt
Wenn die letzte Stammart der Diptera im Larvenstadium tatsächlich schräg ventrad
gerichtete und vertikal bewegliche Mandibeln besessen hat, dann ist die horizontal
bewegliche Beißmandibel der Bibionomorpha als abgeleitet zu bewerten. Da es so gut
wie ausgeschlossen ist, daß die Übereinstimmung in dieser Merkmalsausprägung mit
einigen Tipulidae auf Synapomorphie beruht, kann die horizontal bewegliche Beiß-
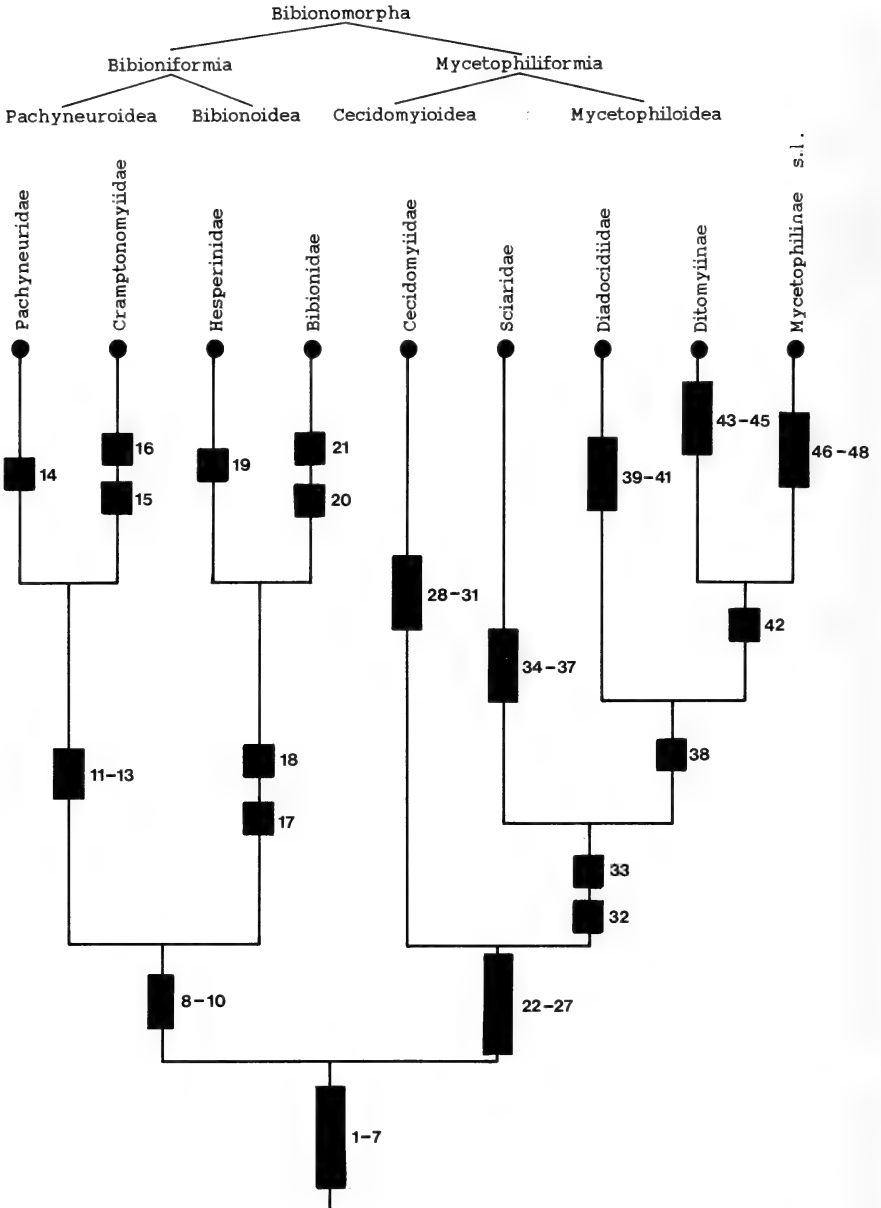
Abb.278: Verwandtschaftsdiagramm der Bibionomorpha: (1) Mandibeln restlos reduziert (Imagines); (2) Larvale Mandibeln werden horizontal bewegt; (3) Costa am Hinterrand des Flügels reduziert; (4) Ejakulator-Apodem in zwei Abschnitte gegliedert (Männchen); (5) Muskel zwischen Gonocoxit und Gonocoxit-Apodem (Männchen); (6) Parameren-Muskel vorhanden (Männchen);

mandibel als Autapomorphie der Bibionomorpha bewertet werden. Diese Hypothese ist erst dann falsifiziert, wenn die mehrfach unabhängige Entstehung vertikal beweglicher Mandibeln innerhalb der Diptera wahrscheinlich gemacht werden kann.

(3) Reduktion der Costa am Hinterrand des Flügels
Diese Merkmalsausprägung, die ohne jeden Zweifel abgeleitet ist, ist als Argument für die Monophylie der Bibionomorpha ähnlich zu bewerten wie Merkmal (1). In beiden Fällen handelt es sich um innerhalb der Diptera häufig auftretende Reduktionen, so daß auch für die Bibionomorpha Konvergenzen nicht ausgeschlossen werden können.

Die drei folgenden Merkmale finden sich im männlichen Genitale, werden aber — da sie nicht miteinander korreliert sind — getrennt aufgeführt:

(4) Ejaculator-Apodem im männlichen Genitale in zwei Abschnitte gegliedert
Da diese Merkmalsausprägung von keinem anderen Taxon außerhalb der Bibionomorpha bekannt ist, kann sie nur als Autapomorphie der Bibionomorpha bewertet werden.

(5) Stabilisierender Muskel zwischen Gonocoxit und Gonocoxit-Apodem (M7)
Auch dieses Muskelpaar findet sich nur innerhalb der Bibionomorpha; diese apomorphe Merkmalsausprägung kann als weiteres Argument für die Monophylie der Bibionomorpha herangezogen werden.

(6) Parameren-Muskel (M9)
Obwohl Parameren zum Grundmuster der Diptera gehören, tritt dieses Muskelpaar nur innerhalb der Bibionomorpha auf. Der Besitz eines Parameren-Muskels ist wahrscheinlich eine weitere Autapomorphie des Taxon, da sonst die vielfache Reduktion des Muskelpaares innerhalb der Diptera angenommen werden müßte.

(7) Episternum des Mesothorax ist asymmetrisch geteilt
Da die beiden potentiellen Adelphotaxa der Bibionomorpha (Brachycera und/oder Blephariceridae) ein annähernd symmetrisch geteiltes Episternum aufweisen, ist es wahrscheinlich, daß die Asymmetrie als autapomorphe Merkmalsausprägung bewertet werden kann.

(7) Episternum des Mesothorax asymmetrisch geteilt (Imagines); (8) Antenne bis auf ein Glied scheibenförmig verkürzt (Larven); (9) Palpus labialis restlos reduziert (Larven); (10) Labium und Hypopharynx miteinander verbunden (Larven); (11) Verschmälerung der Flügelbasis; (12) Paarige, stärker sklerotisierte Bereiche auf dem Prothorax (Larven); (13) Beine stark verlängert (Imagines); (14) Diskoidalzelle fehlt (Flügelgeäder); (15) Metathorakal-Stigma sehr klein (Larven); (16) Querader zwischen den Ästen des Radialsektors (Flügelgeäder); (17) Antennengeißel verkürzt (Imagines); (18) Genitalsegment-Boden durchgehend sklerotisiert (Männchen); (19) Gonostyli apikal tief eingebuchtet (Männchen); (20) Männchen holoptisch; (21) Larvale Cuticula mit Anhängen; (22) Diskoidalzelle fehlt; (23) Radialsektor 2-ästig (Flügelgeäder); (24) Media-Stamm schwach ausgeprägt (Flügelgeäder); (25) Pulvillen reduziert (Imagines); (26) Zwei Spermathekae (Weibchen); (27) Beinscheiden liegen in einer Ebene nebeneinander (Puppen); (28) Kopfkapsel reduziert, Mandibeln stilettförmig (Larven); (29) Ausbildung von Metacephalstäben (Larven); (30) Spatula sternalis (Larven); (31) Cuticula mit Papillen (Larven); (32) Coxae verlängert (Imagines); (33) Tibialorgan (Imagines); (34) Penis mit Dörnchenplatte (Männchen); (35) Gonocoxosternit VIII verlängert (Weibchen); (36) 8. abdominales Stigmenpaar reduziert (Larven); (37) Antenne bis auf ein Glied verkürzt (Larven); (38) Gänge der Spermathekae münden direkt im Genitalkammer-Dach (Weibchen); (39) Radialsektor 1-ästig (Flügelgeäder); (40) Larven propneustisch; (41) Larvale Antenne bis auf ein Glied verkürzt; (42) Postphragma verkürzt (Imagines); (43) Subcosta verkürzt (Flügelgeäder); (44) Palpiger stabförmig (Larven); (45) Tibialorgan nicht grubig differenziert (Imagines); (46) Labialpalpen restlos reduziert (Larven); (47) 8. abdominales Stigma reduziert (Larven); (48) Sternum IX nicht distinkt vorhanden (Männchen).

Unter den sieben mutmaßlichen Autapomorphien der Bibionomorpha ist nicht eine, die als Argument durch besondere Qualität überzeugen könnte. Es liegen mit ihnen aber Indizien vor, die in ihrer Gesamtheit die Existenz der Bibionomorpha als geschlossene Abstammungsgemeinschaft wahrscheinlich machen. Zu dieser Hypothese gibt es beim derzeitigen Kenntnisstand keine begründbare Alternative. Darüberhinaus hat sich gezeigt, daß die Bibionomorpha excl. der Anisopodidae und Scatopsoidea überzeugender als Monophylum begründet werden können als die Bibionomorpha sensu Hennig. Aus diesen Gründen erscheint es gerechtfertigt, mit der Hypothese weiterzuarbeiten, daß die Bibionomorpha (Bibioniformia + Mycetophiliformia) als Monophylum existent sind.

Bibioniformia

Die Bibioniformia, die neben den Bibionoidea auch noch die artenarmen Pachyneuridae umfassen, sind in vielen Merkmalen ursprünglicher geblieben als ihre Schwestergruppe, die Mycetophiliformia. Dementsprechend schwierig ist es, ihre Existenz als geschlossene Abstammungsgemeinschaft zu belegen. Folgende Merkmalsausprägungen weisen aber auf die Monophylie dieser Gruppierung hin:

(8) Larvale Antenne bis auf ein Glied scheibenförmig verkürzt

Zum Grundmuster der Mycetophiliformia gehört eine noch dreigliedrige, spitz-konische larvale Antenne. Bei allen Larven der Vertreter der Bibioniformia ist die Antenne aber bis auf ein Glied verkürzt und dadurch scheibenförmig ausgeprägt. Die Merkmalsverteilung zeigt, daß noch zum Grundmuster der geschlossenen Abstammungsgemeinschaft Bibionomorpha eine larvale Antenne mit 3 Gliedern gehört. Dieser Zustand ist in das Grundmuster der Mycetophiliformia übernommen worden, während in der Stammlinie der Bibioniformia die Reduktion von Antennengliedern weiter fortgeschritten ist. Die letzte Stammart des Taxon hat dann im Larvenstadium eine nur eingliedrige, scheibenförmige Antenne besessen. Diese Merkmalsausprägung kann nur als autapomorpher Merkmalszustand im Grundmuster der Bibioniformia bewertet werden.

(9) Palpus labialis bei den Larven restlos reduziert

Auch das Labium der Larven der Bibioniformia ist gegenüber dem des Grundmusters der Diptera vereinfacht. Die innerhalb der Diptera nur noch selten auftretenden Labialpalpen (Hennig 1973: 105) gehören sicher noch zum Grundmuster der Bibionomorpha, da sie bei den Larven der Ditomyiidae (Mycetophiliformia) (Keilin 1919; Madwar 1937) noch wohlentwickelt vorhanden sind. Die Larven aller Bibioniformia zeichnen sich dagegen durch den vollständigen Mangel eines Palpus labialis aus (Morris 1917; Perraudin 1961; Krivosheina & Mamayev 1967, 1970). Dieser apomorphe Merkmalszustand gehört sicher zum Grundmuster der Bibioniformia und ist als weiteres Indiz für die Monophylie dieses Taxon anzusehen.

(10) Verbindung zwischen Labium und Hypopharynx bei den Larven

Die Larven der Bibioniformia zeichnen sich durch eine besondere Verbindung des Labium mit dem Hypopharynx aus. Bei allen bisher beschriebenen Formen liegt das Praementum eingebettet zwischen lateralen Ausläufern des Hypopharynx (Morris 1917; Perraudin 1961; Krivosheina & Mamayev 1967, 1970). Eine solche Konfiguration ist wohl einmalig innerhalb der Diptera und kann mit großer Sicherheit als autapomorphes Grundmustermerkmal der Bibioniformia bewertet werden.

1. Pachyneuroidea

Die Pachyneuridae umfassen lediglich vier Arten, die zerstreut im holarktischen Raum verbreitet sind: *Pachyneura fasciata* Zetterstedt, 1838; *Haruka elegans* Okada, 1938; *Pergratospes holoptica* Krivosheina & Mamayev, 1970 und *Cramptonomyia spenceri* Alexander, 1931. Während die drei letztgenannten Spezies wohl immer als näher miteinander verwandt betrachtet wurden, sind die Vorstellungen über die Verwandtschaftsbeziehungen von *Pachyneura* sehr verschieden. Sie wurden seit ihrer Beschreibung zu den Bibionidae (Duda 1930), zu den Tipulomorpha sensu Rohdendorf (1964) und zu den Axymyiidae (Hennig 1973: 30) gestellt. Wood (1981) ist der erste gewesen, der alle vier Arten (unter der Familienbezeichnung Pachyneuridae) zusammengefaßt hat. Und tatsächlich weisen auch einige Indizien auf die Monophylie dieser Gruppierung hin:

(11) Verschmälerung der Flügelbasis
Die Flügelbasis ist bei allen vier Arten stark verschmälert, eine Alula ist nicht vorhanden (Krivosheina & Mamayev 1970, Wood 1981). Da ein solcher Lappen am Hinterrande des Flügels aber unzweifelhaft zum Grundmuster der Bibionomorpha — wie die Bibionoidea und Mycetophiliformia zeigen — gehört, kann diese Reduktion als autapomorphe Übereinstimmung der Pachyneuroidea bewertet werden.

(12) Larvaler Prothorax
Die Larven der Pachyneuridae zeichnen sich durch den Besitz von paarigen, stärker sklerotisierten Bereichen auf der Dorsal- und Ventralseite des Prothorax aus (Krivosheina & Mamayev 1970, 1986); nach Wood (1981) sollen sie als Ansatzstellen für Muskeln dienen, die an der Drehung des Kopfkapsel beteiligt sind. Eine solche Differenzierung des Prothorax ist innerhalb der Bibionomorpha nicht noch einmal zu finden und scheint auch für die Larven aus anderen Taxa der Diptera nicht bekannt zu sein. Aus diesem Grunde ist es ohne Widerspruch möglich, diese Merkmalsausprägung als Autapomorphie im Grundmuster der Pachyneuroidea zu werten.

(13) Beine der Imagines stark verlängert
Bei allen vier Arten der Pachyneuridae sind die Beine auffallend stark verlängert. Diese Merkmalsausprägung ist innerhalb der Diptera sehr oft unabhängig entstanden und daher mit Vorsicht zu betrachten. Es scheint aber nicht sinnvoll zu sein, diese Übereinstimmung innerhalb der Pachyneuroidea als Folge konvergenter Entwicklung betrachten zu wollen. Darüberhinaus sind weder die Beine der Bibionoidea noch der Mycetophiliformia im Grundmuster so extrem (tipulidenartig) verlängert wie bei diesem Taxon. Daher kann dieser Merkmalszustand als weitere Autapomorphie der Pachyneuroidea bewertet werden. — Desweiteren weisen Wood & Borkent (1989: 1350) auf synapomorphe Übereinstimmungen im Bereich der männlichen Genitalien hin, ohne aber im Detail darauf einzugehen.

1.1. Pachyneuridae

(14) Diskoidalzelle reduziert
Die monotypische Gattung *Pachyneura* unterscheidet sich von den übrigen Arten der Pachyneuroidea durch das Fehlen der Diskoidalzelle im Flügelgeäder. Diese Besonderheit ist sicher apomorph.

1.2. Cramptonomyiidae

(15) Metathorakal-Stigma der Larven sehr klein
Während bei *Pachyneura* das Stigma des Metathorax so groß ist wie die übrigen Atem-

öffnungen, ist es bei den drei Arten der Cramptonomyiidae stark verkleinert und bei *Pergratospes* kaum zu erkennen (Krivosheina & Mamayev 1970). Da ein deutlich holopneustisches Tracheensystem Grundmuster-Merkmal der Bibionomorpha ist, kann Verkleinerung des metathorakalen Stigmas als Autapomorphie der Cramptonomyiidae bewertet werden.

(16) Querader zwischen den Ästen des Radialsektors
Dies ist eines der seltenen Beispiele dafür, daß Merkmale des Flügelgeäders nicht immer Reduktionen sind. Auch wenn die Deutung dieser „überzähligen" Ader nicht eindeutig erfolgen kann, ist der Besitz der Querader ein abgeleiteter Merkmalszustand (Wood 1981). Damit liegt ein weiteres Indiz für die Monophylie der Cramptonomyiidae vor.

2. Bibionoidea

(17) Antennengeißel verkürzt
Wieviele Glieder die Antennengeißel der letzten Stammart der Diptera besessen hat, läßt sich verläßlich nur schwer bestimmen. Innerhalb der Diptera tritt am weitaus häufigsten die Zahl 14 auf, so daß im allgemeinen Formen sowohl mit weniger als auch mit mehr Geißelgliedern als abgeleitet betrachtet werden (Hennig 1973: 164). Bei den Bibionoidea treten immer nur maximal zehn Antennengeißel-Glieder in Erscheinung (Hennig 1973: 31), während bei den Pachyneuroidea und den Mycetophiliformia die Zahl 14 vorherrschend ist. Diese Merkmalsverteilung macht wahrscheinlich, daß es eine letzte gemeinsame Stammart von Hesperinidae und Bibionidae gegeben hat und daß diese eine nur 10gliedrige Antennengeißel besaß. Die Ausprägung der Antenne ist damit als ein autapomorphes Grundmuster-Merkmal der Bibionoidea zu bewerten.

(18) Männliche Terminalia mit durchgehend sklerotisierter Ventralfläche des Genitalsegments
Sowohl bei den Hesperinidae (Hardy 1945; Hardy & Takahashi 1960) als auch bei allen Bibionidae sind die Gonocoxite auf der Ventralseite miteinander verschmolzen. Dies ist sicher abgeleitet, denn der ursprüngliche Zustand mit membranöser Ventralfläche findet sich innerhalb der Bibioniformia noch bei den Cramptonomyiidae. Da eine durchgehende Sklerotisierung auch noch nicht zum Grundmuster der Mycetophiliformia gehört, kann diese Merkmalsausprägung als weitere Autapomorphie der Bibionoidea bewertet werden.

2.1. Hesperinidae

Dieses Taxon, das nur die holarktisch verbreitete Gattung *Hesperinus* Walker, 1848 umfaßt, läßt sich durch eine Autapomorphie aus dem Bereich des männlichen Genitale zufriedenstellend als geschlossene Abstammungsgemeinschaft begründen:

(19) Gonostyli im männlichen Genitale tief eingebuchtet
Diese Merkmalsausprägung, auf die bereits Hennig (1973: 31) hingewiesen hat, ist eindeutig apomorph. Ähnliche Gonostyli finden sich noch innerhalb der Mycetophilidae, doch sind sie nicht Bestandteil des Grundmusters der Mycetophiliformia. So ist es zweifelsfrei möglich, die gegabelten Gonostyli von *Hesperinus* als Autapomorphie des Taxon zu bewerten.

2.2. Bibionidae (Abb.279)

Die weltweit verbreiteten Bibionidae sind als geschlossene Abstammungsgemeinschaft zufriedenstellend zu begründen:

(20) Männchen holoptisch
Diese auffällige Merkmalsausprägung ist nach Hennig (1973: 31) eine Autapomorphie der Bibionidae.

(21) Cuticula der Larven mit fleischigen Anhängen
Nach Hardy (1981) und Krivosheina (1086: 314, 319) sind solche Anhänge, die sich über die gesamte Körperoberfläche verteilen, typisch für die Bibionidae, während ihrem Adelphotaxon, den Hesperinidae, solche Differenzierungen fehlen. Auch in der weiteren Außengruppe ist diese Merkmalsausprägung nicht zu finden. Daher ist es möglich, den Besitz von fleischigen Anhängen als Autapomorphie der Bibionidae zu werten.

Innerhalb der Bibionidae können die **Bibioninae** besonders gut als geschlossene Abstammungsgemeinschaft ausgewiesen werden:

(—) Vorderschenkel der Imagines verdickt
Diese von Hennig (1973: 31) angeführte Merkmalsausprägung ist sicher autapomorph, da die Femora in der Außengruppe nicht auffallend verdickt sind.

(—) Im Flügelgeäder ist der Radialsektor 1-ästig
Da im Grundmuster der Bibionoidea und auch in dem der Bibionidae der Radialsektor zwei Äste aufweist (Hennig 1973: 31), kann die Einästigkeit bei den Bibioninae als weiteres Indiz für ihre Monophylie angesehen werden.

(—) 8. abdominales Stigmenpaar in beiden Geschlechtern dorsad in den Bereich des 9. Segments verlagert
Die Verschiebung des ursprünglich in der Pleuralmembran gelegenen Stigmenpaares erfolgte wahrscheinlich erst in der Stammlinie der Bibioninae und ist damit eine Autapomorphie des Taxon. Die übrigen Bibionidae und auch *Hesperinus* haben dieses Stigmenpaar reduziert. Es scheint unwahrscheinlich, daß diese Reduktion erst nach erfolgter Verlagerung dorsad erfolgt ist. Und auch wenn es sich beim letzten abdominalen Stigmenpaar der Bibioninae um einen Neuerwerb handeln sollte, ist es immer noch als Autapomorphie zu bewerten.

(—) Tergum X der Legeröhre restlos reduziert
Diese Merkmalsausprägung, die für alle bislang untersuchten Weibchen der Bibioninae typisch ist (Iwata & Nagatomi 1979), ist sicher eine weitere Autapomorphie des Taxon. Denn sowohl die übrigen Bibionidae als auch *Hesperinus* (Iwata & Nagatomi 1981) repräsentieren durch den Besitz des Tergum X den ursprünglichen Zustand.

(—) Cerci der Weibchen eingliedrig
Die Bewertung, daß es sich hierbei um eine weitere Autapomorphie der Bibioninae handelt, läßt sich wie beim vorhergehenden Merkmal begründen.

(—) Vasa deferentia verdickt und verkürzt
Bislang sind die inneren Geschlechtsorgane nur bei wenigen Arten der Bibionidae untersucht worden, so daß die Bewertung der Merkmalsausprägung als Autapomorphie der Bibioninae mit Vorsicht zu betrachten ist.

Die übrigen Bibionidae, in der konventionellen Klassifikation als Pleciinae zusammengefaßt, lassen sich dagegen nicht als monophyletische Gruppe begründen (Hennig 1973: 31). Es soll aber bemerkt werden, daß bei den vier Arten der Pleciinae *(Penthetria funebris, Plecia ornaticornis, P. amplipennis, P. nearctica* [Leppla et al. 1975]), deren Penis genauer untersucht ist, das Dorsalsklerit ein gut entwickeltes mediales Apodem
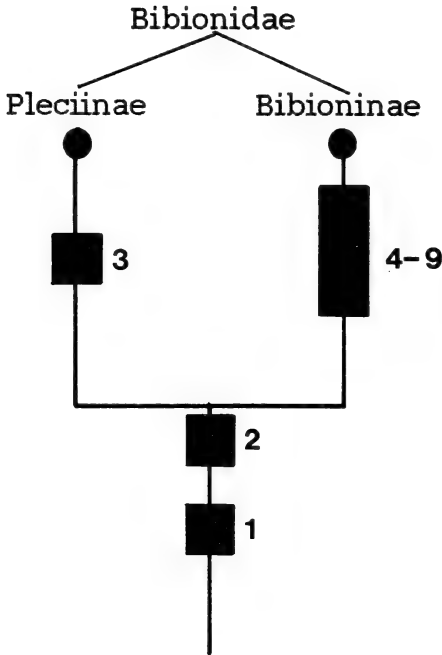
Abb.279: Die basale Verzweigung im Verwandt-schaftsdiagramm der Bibionidae (Erläuterungen zu den Apomorphien vgl. Text): (1) Männchen holoptisch; (2) Larvale Cuticula mit Anhängen; (3) Dorsalsklerit mit medialem Apodem (Männchen); (4) Vorderschenkel der Imagines verdickt; (5) Radialsektor 1-ästig (Flügelgeäder); (6) 8. abdominales Stigmenpaar dorsad verlagert (Imagines); (7) Tergum X der Weibchen restlos reduziert; (8) Cerci der Weibchen eingliedrig; (9) Vasa deferentia (Männchen) verkürzt und verdickt.

aufweist. Das könnte darauf hinweisen, daß es sich doch um ein Monophylum und nicht um eine paraphyletische Restgruppe handelt.

Mycetophiliformia

Das stammesgeschichtliche Gegenstück zu den Bibioniformia sind die artenreichen Mycetophiliformia, zu denen die Cecidomyiidae, Sciaridae, Diadocidiidae und Mycetophilidae gehören. Als geschlossene Abstammungsgemeinschaft sind die Mycetophiliformia überwiegend durch Reduktions-Erscheinungen gekennzeichnet. Die folgenden drei Autapomorphien sind Reduktionen des Flügelgeäders (Hennig 1954):

(22) Im Flügelgeäder fehlt die Diskoidalzelle

(23) Radialsektor 2-ästig

(24) Media-Stamm schwach ausgeprägt

(25) Pulvillen reduziert
Bei den Bibioniformia sind die Pulvillen ebenso lang wie das Empodium, was wahrscheinlich dem Grundmuster der Bibionomorpha entspricht. Daher ist es möglich, die Reduktion der Pulvillen als Autapomorphie der Mycetophiliformia zu bewerten.

(26) Weibchen mit zwei Spermathecae
Dies ist sicher eine weitere Autapomorphie der Mycetophiliformia, da im Grundmuster der Bibioniformia mit drei Spermathecae noch der ursprüngliche Zustand repräsentiert ist.

(27) Beinscheiden der Puppen liegen in einer Ebene nebeneinander
Diese Merkmalsausprägung ist vermutlich ebenfalls eine Autapomorphie der Myceto-
philiformia, da in der engeren (übrige Diptera) und weiteren Außengruppe eine Überla-
gerung der Beinscheiden dominiert.

Innerhalb der Mycetophiliformia besteht ein Schwestergruppen-Verhältnis zwischen
den Cecidomyioidea und den Mycetophiloidea.

1. Cecidomyioidea

Dieses artenreiche, weltweit verbreitete Taxon ist mit wünschenswerter Sicherheit eine
geschlossene Abstammungsgemeinschaft. Hennig (1973: 32) führt folgende Merkmals-
ausprägungen auf, die eindeutig als Autapomorphien bewertet werden können:

**(28) Kopfkapsel der Larven reduziert, die Mandibeln sind stilettförmig, die Maxillen
sind reduziert**

(29) Ausbildung von Metacephalstäben, die bis in den Prothorax ragen (Larven)

(30) Besitz einer Spatula sternalis („Brustgräte") (Larven)

(31) Cuticula der Larven mit einer Papillen-Garnitur

2. Mycetophiloidea

Das Adelphotaxon der Cecidomyioidea sind die Mycetophiloidea. In diesem Taxon sind
Sciaridae, Diadocidiidae und Mycetophilidae zusammengefaßt. Die Monophylie der
Mycetophiloidea ist mit einiger Sicherheit begründbar:

(32) Verlängerte Coxen
Die Coxae sind in beiden Geschlechtern im Verhältnis zur Thorax-Höhe extrem verlän-
gert. Dies ist sicher als Autapomorphie der Mycetophiloidea zu bewerten.

(33) Tibialorgan
Der Besitz einer grubigen Differenzierung, die in Verbindung mit einer Drüsenplatte an
der Medialseite der Vorder-Tibia auftritt, ist eindeutig als Autapomorphie zu werten, da
außerhalb der Mycetophiloidea ein so strukturiertes Tibialorgan nicht zu finden ist.

2.1. Sciaridae

Dieses weltweit verbreitete, verhältnismäßig artenarme Taxon ist sehr gut als monophy-
letische Einheit zu begründen:

(34) Penis mit Dörnchenplatte
Der verbreiterte caudale Teil des Ejaculator-Apodems ist bei allen bislang beschriebe-
nen Sciaridae als Dörnchenplatte ausgebildet: auf der Ventralseite befinden sich abge-
flachte Dörnchen, deren Spitzen alle craniad gerichtet sind. Diese Merkmalsausprä-
gung ist innerhalb der Diptera einmalig und somit ohne Widerspruch als Autapomor-
phie der Sciaridae bewertbar.

(35) Gonocoxosternit VIII caudad bis in den Bereich des 10. Segments verlängert
Diese Verlängerung innerhalb der Legeröhre, die mit der Verlagerung des Gonotrema
korreliert ist, kann mit Sicherheit als autapomorphe Merkmalsausprägung angesehen
werden, da die übrigen Bibionomorpha darin noch dem Grundmuster der Diptera ent-
sprechen.

Die folgenden Merkmalsausprägungen lassen sich auf Reduktionen zurückführen, die stark konvergenzverdächtig sind. Daher sind sie zur Begründung der Monophylie der Sciaridae nur bedingt brauchbar.

(36) 8. abdominales Stigmenpaar restlos reduziert (Larven)
Diese Merkmalsausprägung findet sich innerhalb der Mycetophilidae häufiger, seine Bewertung kann nur mit Hilfe des Verwandtschaftsdiagramms erfolgen.

(37) Larvale Antenne bis auf ein scheibenförmiges Glied verkürzt
Auch diese Reduktion ist innerhalb der Bibionomorpha häufiger anzutreffen, gehört aber nicht zum Grundmuster der Mycetophiliformia, da die Cecidomyioidea und einige Mycetophilidae noch dreigliedrige Antennen besitzen. Auch in diesem Fall erfolgte die Bewertung als Autapomorphie der Sciaridae anhand des Verwandtschaftsdiagramms.

2.2. Mycetophilidae s.l.

Diadocidiidae und Mycetophilidae sind eine geschlossene Abstammungsgemeinschaft (Mycetophilidae s.l.). Diese Hypothese läßt sich lediglich über ein Merkmal begründen, das aber in seiner Aussagekraft beachtenswert ist:

(38) Die Gänge der beiden Spermathecae münden nebeneinander direkt im Dach der Genitalkammer
Diese Merkmalsausprägung, die durch den Verlust des unpaaren Ductus Spermathecae erklärt werden kann, ist einmalig innerhalb der Bibionomorpha. Auch für andere Dipteren ist dieser Merkmalszustand unbekannt. Daher ist das Merkmal mit Sicherheit eine Autapomorphie der Mycetophilidae s.l.

2.2.1. Diadocidiidae

Nach Hennig (1973: 34) werden die Gattungen *Diadocidia* (zehn Arten in der Holarktis, in Tasmanien und im südlichen Südamerika) und *Pterogymnus* (1 Art in Südchile) als Diadocidiidae zusammengefaßt. Diese Gruppierung ist aber nicht als Monophylum zu begründen. Das hängt damit zusammen, daß die entscheidende Autapomorphie von *Diadocidia* ein larvales Merkmal ist, von *Pterogymnus* aber nur die weibliche Imago bekannt ist (Freeman 1951: 11). Aus diesem Grunde ist es sinnvoll, *Pterogymnus* vorläufig aus den Diadocidiidae herauszunehmen und als Taxon incertae sedis zu kennzeichnen. Der Rest der Diadocidiidae *(Diadocidia)* ist durch folgende Autapomorphien (Hennig 1954, 1973: 34; Plachter 1979b) als Monophylum begründbar:

(39) Radialsektor im Flügelgeäder 1-ästig

(40) Larven mit propneustischem Tracheensystem

(41) Larvale Antennen bis auf ein Glied reduziert

2.2.2. Mycetophilidae s.str.

Dieses Taxon umfaßt alle übrigen Pilzmücken (Ditomyiinae, Keroplatinae, Bolitophilinae, Manotinae, Sciophilinae und Mycetophilinae). Es ist durch eine Autapomorphie als geschlossene Abstammungsgemeinschaft ausgewiesen:

(42) Postphragma verkürzt
Das endoskelettale Postphragma des Thorax ragt nicht mehr bis in das 1. abdominale Segment; diese Merkmalsausprägung ist sicher autapomorph, da im Grundmuster der Mycetophiliformia noch der ursprüngliche Zustand (Postphragma ragt bis in das 1. abdominale Segment) repräsentiert ist.

Beim derzeitigen Kenntnisstand läßt sich innerhalb der Mycetophilidae s.str. noch die basale Verzweigung des Taxon auflösen. Weiterführende Analysen scheitern daran, daß die sehr formenreiche Gruppierung der Sciophilinae nicht als Monophylum begründet werden, aber auch nicht als paraphyletische Gruppe aufgelöst werden kann.

2.2.2.1. Ditomyiinae (Abb.280)

Die Ditomyiinae sind die Schwestergruppe zu den übrigen Mycetophilidae s.str. Das ist deswegen von Interesse, da die Ditomyiinae bislang als das ursprünglichste Taxon der Mycetophiloidea oder gar der Mycetophiliformia (Griffiths, in litt.) angesehen wurden. Der Grund dafür ist der Besitz einiger ursprünglicher Merkmale wie z. B. bei den Larven das Vorhandensein des Palpus labialis, einer dreigliedrigen Antenne und des 8. abdominalen Stigmenpaares. Die Plazierung der Ditomyiinae innerhalb der Mycetophilidae s.str. hat zur Folge, daß die Reduktion dieser larvalen Merkmale bei den Mycetophiliformia mehrfach unabhängig erfolgt sein muß.

Folgende Gattungen werden als Ditomyiinae zusammengefaßt:
Ditomyia Winnertz, *Asioditomyia* Saigusa, *Symmerus* Walker (Holarktis)
Celebesomyia Saigusa (Palaearktis)
Rhipidita Edwards, *Neoditomyia* Lane & Sturm, *Calliceratomyia* Lane (Neotropis)
Nervijuncta Marshall, *Australosymmerus* Freeman (Australis, Neotropis)

Das Problem bei der Begründung der Ditomyiinae als geschlossene Abstammungsgemeinschaft liegt hauptsächlich darin, daß komplexere Merkmale wie die männlichen Terminalia und die Mundwerkzeuge der Larven nur lückenhaft untersucht sind. Dies betrifft in erster Linie die neotropisch verbreiteten Genera, von denen weder ausreichend fixiertes Material zugänglich ist noch die präimaginalen Stadien bekannt sind.

Für die Monophylie der Ditomyiinae sprechen die folgenden abgeleiteten Merkmalsausprägungen:

(43) Im Flügelgeäder ist die Subcosta verkürzt
Sie erreicht weder die Costa noch R1 (Hennig 1954: 305). Dies ist zwar ein sehr einfaches Merkmal, ist dafür aber von allen beschriebenen Ditomyiidae bekannt.

(44) Larvale Maxille mit stabförmigen Palpiger
Plachter (1979) wies darauf hin, daß sich die Maxille der Ditomyiinae stark von der aller übrigen Mycetophilidae unterscheidet. Abgeleitet sind dabei sicher die weitgehende Reduktion der Galea, das Fehlen der Lacinia und die stabförmige Ausprägung des Pal-
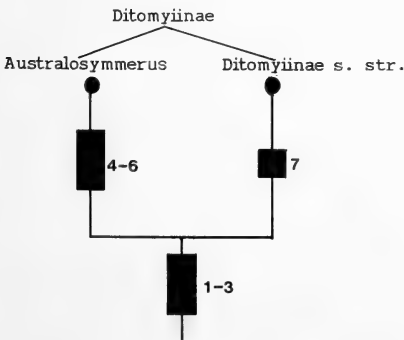
Abb.280: Die basale Verzweigung im Verwandtschaftsdiagramm der Ditomyiinae (Erläuterungen zu den Apomorphien vgl. Text): (1) Subcosta verkürzt (Flügelgeäder); (2) Stabförmiger Palpiger (Larven); (3) Tibialorgan nicht grubig differenziert (Imagines); (4) Gonostylus (Männchen) komplex differenziert; (5) Tergum IX mindestens ebenso lang wie die Gonocoxite (Männchen); (6) Cerci postero-laterad verlagert (Männchen); (7) Pteropleura stark eingeengt, erreicht nicht die Basis des Thorax (Imagines).

piger. Bekannt ist diese apomorphe Merkmalskombination von *Ditomyia fasciata* (Keilin 1919; Madwar 1937), *Symmerus annulatus* (Keilin 1919) und *Australosymmerus* spec. (Madwar 1937).

(45) Tibialorgan ist nicht grubig differenziert
Diese Merkmalsausprägung ist nur dann als Autapomorphie bewertbar, wenn das Tibialorgan der letzten Stammart der Mycetophiloidea grubig differenziert gewesen ist. Sollte dagegen die Grube mit den Borstenreihen erst innerhalb der Mycetophilidae aus einem einfacher gebauten Tibialorgan entstanden sein, dann repräsentieren die Ditomyiinae noch den ursprünglichen Zustand. Gegen diese Alternative spricht aber, daß die meisten Arten der Ditomyiinae überhaupt kein Tibialorgan besitzen.

Aufgrund dieser drei Merkmalsausprägungen können die Ditomyiinae als Monophylum ausgewiesen werden, der gegenwärtige Kenntnisstand läßt keine andere Interpretation zu.

Australosymmerus ist das Adelphotaxon zu allen übrigen Ditomyiinae. Diese sind durch eine Autapomorphie als Monophylum begründbar:

(—) Die Pteropleura stark eingeengt und erreicht nicht die Basis des Thorax
Die Ausprägung der lateralen Thorax-Sklerite ist von allen Vertretern der Ditomyiinae bekannt, so daß diese Autapomorphie gesichert ist.

Die Monophylie von *Australosymmerus* ist nach Munroe (1974) gut begründet:

(—) Gonostylus komplex differenziert
Der Gonostylus ist in seiner Größe reduziert, apikal erweitert und mit einer typischen Zähnchenplatte versehen.

(—) Tergum IX ist mindestens so lang wie die Gonocoxite

(—) Cerci bilden nicht die laterale Abgrenzung des Analkomplexes, sondern sind postero-laterad verlagert

Der Hypothese, daß *Australosymmerus* und *Symmerus* Schwestergruppen seien (Munroe 1974), läßt sich einiges entgegensetzen. Die Übereinstimmung bezüglich der Ausbildung einer Augenbrücke beruht klar auf Symplesiomorphie, da der Besitz einer Augenbrücke bereits Grundmuster-Merkmal der Mycetophiliformia sein muß. Die Verlängerung der Cerci bei den Männchen kann auch als konvergente Entwicklung gedeutet werden, da einige Arten von *Australosymmerus* kleine Cerci besitzen. Selbstverständlich ist denkbar, daß es sich hierbei um eine sekundäre Größenreduktion handelt. Diese Annahme steht aber im Konflikt mit der Ausprägung der Thoraxseitenwand und der Ausprägung der inneren Geschlechtsorgane bei den Männchen. Während der Ductus ejaculatorius von *Australosymmerus* in Länge und Bemuskelung noch dem Grundmuster der Bibionomorpha entspricht, stimmen *Symmerus* und *Ditomyia* in einem abgeleiteten Merkmalszustand überein: der Ductus ejaculatorius ist (weitgehend) paarig ausgeprägt.

2.2.2.2. Mycetophilinae s.l.

Diese Restgruppe ist als Monophylum kaum zufriedenstellend zu begründen. Alle Merkmalsausprägungen, die als Autapomorphien bewertet werden könnten, sind Reduktionen, die besonders konvergenzverdächtig sind. Da es beim derzeitigen Kennt-

nisstand aber keine begründbare Alternative gibt, soll diese Gruppe vorläufig und unter Vorbehalt als geschlossene Abstammungsgemeinschaft angesehen werden:

(46) Larvale Labialpalpen reduziert

(47) 8. abdominales Stigma reduziert

(48) Sternum IX im männlichen Genitale als distinktes Element nicht mehr vorhanden

Diese Merkmalsausprägungen sind ohne Zweifel abgeleitet, aber es ist unsicher, ob sie auf Synapomorphie oder Konvergenz beruhen. Zur Klärung dieser Frage ist die Analyse der nicht als Monophylum begründbaren, formenreichen Sciophilinae unbedingt notwendig.

In der Methodik der Phylogenetischen Systematik folgt — als letzter Schritt — auf die Rekonstruktion der Cladogenese die Umsetzung des Verwandtschaftsdiagramms direkt in ein geschriebenes System. Der jetzige Kenntnisstand über die verwandtschaftlichen Beziehungen innerhalb der Bibionomorpha ist aber nicht ausreichend, um das System eines so artenreichen Taxon zu schreiben. Das vorgelegte Verwandtschaftsdiagramm bedarf noch der weiteren Überprüfung und Bestätigung anhand anderer Merkmalskomplexe, so daß eine Abänderung des konventionellen Systems — im Sinne der Stabilität — verfrüht erscheint.

Widersprüche in der Rekonstruktion der verwandtschaftlichen Beziehungen

Bezüglich der Cecidomyiidae und Sciaridae gerät das vorgelegte Verwandtschaftsdiagramm in Konflikt mit einer anderen, weithin akzeptierten Hypothese. Kernpunkt dieser ist die Annahme eines Schwestergruppen-Verhältnisses beider Taxa. Begründet ist dies durch cytologische Besonderheiten (White 1957). Sowohl bei den Cecidomyiidae als auch bei den Sciaridae treten in der Keimbahn überzählige Chromosomen auf. Da dieses Phänomen aber auch von Chironomidae (Orthocladiinae) bekannt ist (Bauer & Beermann 1952), muß auch an das Vorliegen konvergenter Verhältnisse gedacht werden.

Wird die — sicher abgeleitete — chromosomale Besonderheit bei Cecidomyiidae und Sciaridae auf Synapomorphie zurückgeführt, so ergeben sich folgende Konsequenzen:
— Tibialorgan (33) und die Verlängerung der Coxen (32) sind innerhalb der Mycetophiliformia zweimal unabhängig entstanden; einmal in der Stammlinie der Sciaridae und einmal in der Stammlinie der Mycetophilidae s.l. Für die Merkmalsausprägung der Coxae ist diese Hypothese durchaus wahrscheinlich, für das Tibialorgan aber nicht. Zu groß sind die Übereinstimmungen in Lage, cuticularer Differenzierung und Histologie. Alternativ bleibt noch die Möglichkeit, daß
— das Tibialorgan (und vielleicht auch die verlängerten Coxen) bereits zum Grundmuster der Mycetophiliformia gehört, aber in der Stammlinie der Cecidomyiidae wieder vollständig reduziert worden ist. Begründen läßt sich diese Hypothese nicht, auch nicht mit der Verzwergung der Gallmücken; viele der verhältnismäßig ursprünglichen Lestremiinae sind größere Tiere, aber ein Tibialorgan ist auch bei ihnen nie beschrieben worden.

Die Abschätzung der Wahrscheinlichkeit führt zu dem Ergebnis, daß das Auftreten überzähliger Chromosomen bei Cecidomyiidae und Sciaridae auf Konvergenz zurückzuführen ist. Die apomorphe Übereinstimmung im Besitz des Tibialorgans favorisiert die Hypothese, daß die Sciaridae das Adelphotaxon der Mycetophilidae s.l. sind.

Bibionomorpha Blephariceridae Brachycera
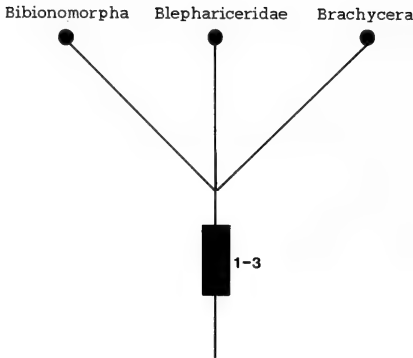
Abb.281: Die potentiellen Adelphotaxa der Bibionomorpha (Erläuterungen zu den Apomorphien vgl. Text): Die Trichotomie ist beim derzeitigen Kenntnisstand nicht auflösbar. Begründung der Monophylie von Brachycera und Blephariceridae vgl. Hennig 1973 (: 22, 35, 36). (1) Laterotergite des Thorax vergrößert (Imagines); (2) Postphragma ungeteilt (Imagines); (3) Dorsalsklerit (Männchen).

Die Stellung der Bibionomorpha innerhalb der Diptera (Abb.281)

Die als Arbeits-Hypothese zugrundegelegte Annahme, daß die Bibionomorpha näher mit den Blephariceridae und Brachycera verwandt sind als mit anderen nematoceren Diptera (Colless & McAlpine 1970), läßt sich mit einem weiteren Merkmal erhärten. Sowohl die Blephariceridae (Zwick 1977) als auch die Brachycera (Nagatomi 1984) zeichnen sich im Grundmuster durch den Besitz eines Dorsalsklerits (Tegmen) im männlichen Genitale aus. Es gibt beim derzeitigen Kenntnisstand keinen Grund zu der Annahme, daß diese Übereinstimmung auf Konvergenz zurückzuführen sei, da das Sklerit bei allen drei Taxa in seiner Lage innerhalb des Penis und in der Verbindung zum Gonocoxit-Apodem übereinstimmt. Da es darüberhinaus immer noch nicht möglich ist, die nematoceren Diptera als geschlossene Abstammungsgemeinschaft zu begründen, ist es wahrscheinlich, daß sie eine paraphyletische Restgruppe darstellen. Ein Teil von ihnen, Bibionomorpha und Blephariceridae, ist näher mit den Brachycera verwandt (sowohl die Monophylie der Blephariceridae als auch der Brachycera ist mit Sicherheit belegbar; vgl. Hennig [1973: 22, 35]). Die Trichotomie dieser Taxa ist zur Zeit aber noch nicht auflösbar. Folgende autapomorphen Merkmalsausprägungen machen die Existenz eines Monophylum Bibionomorpha + Blephariceridae + Brachycera wahrscheinlich (vgl. Abb.281):

(1) Laterotergit des Thorax vergrößert
(2) Postphragma ungeteilt
Beide Merkmalsausprägungen, auf die zuerst Colless & McAlpine (1970) aufmerksam gemacht haben, sind sicher apomorph. Da aber die Anisopodidae und Scatopsoidea (Colless & McAlpine arbeiteten noch mit den Bibionomorpha sensu Hennig) diese Merkmalszustände ebenfalls aufweisen, ist ihre Bewertung als Autapomorphie der Bibionomorpha + Blephariceridae + Brachycera nicht sicher. Es kann sein, daß identische Merkmalsausprägungen konvergent bei Anisopodidae und Scatopsoidea evolviert wurden. Es ist aber auch durchaus möglich, daß homologe Merkmale vorliegen und Anisopodidae und Scatopsoidea das Adelphotaxon der Bibionomorpha + Blephariceridae + Brachycera sind. Dieses Problem kann nur gelöst werden, wenn die Taxa der Psychodomorpha sensu Hennig (1973) im Zusammenhang mit der Stellung der Anisopodidae und Scatopsoidea einer neuen, detaillierten Analyse mit der Methode der Phylogenetischen Systematik unterzogen werden.

(3) Die Dorsalwand des Penis als unpaare Platte ausgebildet, die in Verbindung mit den Gonocoxit-Apodemen steht

Der Besitz eines Dorsalsklerits ist sicher abgeleitet und es spricht nichts gegen seine Bewertung als Autapomorphie eines Taxon Bibionomorpha + Blephariceridae + Brachycera.

ZUSAMMENFASSUNG

Für die Rekonstruktion der Stammesgeschichte der Bibionomorpha werden insgesamt 39 Arten aus nahezu allen höheren Taxa („Familien" der Klassifikation) vergleichend anatomisch untersucht. Im Mittelpunkt stehen dabei Merkmale der männlichen und weiblichen Terminalia, aber auch Thorax und Extremitäten sind einbezogen.

Morphologie

Im männlichen Genitale besteht der Penis aus zwei sklerotisierten Elementen: Dorsalsklerit und Ejaculator-Apodem; unabhängig vom Modus des Spermatransfer sind diese beiden Elemente immer vorhanden. Das Dorsalsklerit ist den Parameren der übrigen Diptera homolog.

Der ursprüngliche Modus des Spermatransfer ist für die Bibionomorpha die Übertragung von Spermatophoren. Innerhalb des Taxon wird dieser Modus abgewandelt, was mit der Evolution von Spermapumpen verschiedenen Typs verbunden ist. Dieser Befund stützt die Annahme, daß Bildung und Übertragung von Spermatophoren noch ein Grundmuster-Merkmal der Diptera ist.

Sowohl das Exoskelett der weiblichen Genitalien als auch der Bau der Genitalkammer entsprechen im Grundmuster der Bibionomorpha der letzten Stammart der Diptera. Erst innerhalb der Bibionomorpha finden Veränderungen, meist Reduktionen, statt.

Entgegen den Angaben in der Literatur ist das Tibialorgan, welches sich subapikal an den vorderen Tibiae der Sciaridae und Mycetophilidae befindet, kein Sinnesorgan. Es handelt sich vielmehr um ein einfach gebautes Drüsenorgan: hinter einer cuticularen Differenzierung befindet sich eine epitheliale Drüsenplatte.

Phylogenie

Die Phylogenie der Bibionomorpha (non sensu Hennig) kann durch eine Reihe von Autapomorphien aus verschiedenen Merkmalsbereichen belegt werden. Eine begründete Hypothese zu den verwandtschaftlichen Beziehungen innerhalb der Bibionomorpha wird vorgelegt.

Wahrscheinlich bilden die Bibionomorpha zusammen mit Blephariceridae und Brachycera eine geschlossene Abstammungsgemeinschaft; demnach sind die „Nematocera" der konventionellen Klassifikation eine paraphyletische Gruppe.

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ANHANG

Liste der verwendeten Abkürzungen

aD	akzessorische Drüse	Gf	Genitalfurca
aE	apikale Differenzierung des Ejakula-tor-Apodems	Gh	Gelenkhaut
Aes	Anepisternum	Gk	Genitalkammer
aGs	apikale Differenzierung des Gonosty-lus	GkDa	Genitalkammer-Dach
		Gkp	Genitalkapsel
Ak	Analkegel	GkpA	Genitalkapsel-Apodem
Ap	Apophyse	Gs	Gonostylus
Apn	Antepronotum	GsSpl,2	Gonostylus-Spange 1,2
AV	Ventralapodem	Gx VIII	Gonocoxosternit VIII
aZ	akzessorisches Zangenpaar	Ha	Haar
		Hal	Halteren-Ansatz
B	ventrale Wand (=Boden) des Genital-segments	Ho	Hoden
		Hp	Hypoproct
Bo	Borste	JGA	Jugum der Gonocoxit-Apodeme
Bob	Borstenbecher		
Bpl	Basalplatte	Kes	Katepisternum
Bx	Bursa copulatrix	Lat	Laterotergit
C	Cercus	lGF	lateraler Gonocoxit-Fortsatz
C1, 2	Cercus-Glied 1, 2	lL	laterale Lamelle
Co	Conjunctiva	lLe	laterale Leiste
caA	caudales Apodem	lPw	laterale Peniswand
crA	craniales Apodem	Ls	Lamellensaum
crF	craniales Foramen	lSp	laterale Spange
Cu	Cuticula	M1-18	Muskel 1-18
Cx	Coxa	m	membranös
Db	Dorsalbrücke	Ma	Muskelansatz
dcF	dorso-caudales Foramen	MaD	Mündung der akzessorischen Drüse
De	Ductus ejaculatorius	meA	medianes Apodem
Ded	Ductus ejaculatorius distalis	Met	Mediotergit
dL	dorsale Lamelle	mGF	medianer Gonocoxit-Fortsatz
Dö	Dörnchenplatte	mlGF	medio-lateraler Gonocoxit-Fortsatz
Dpl	Drüsenplatte	MSpth	Mündung des Ductus Spermathecae
dPl	dorsale Platte	Pa	Parameren
Ds	Dorsalsklerit	PaL	Parameren-Lamelle
dSp	dorsale Spange	Pat	Paratergit
E	Ejaculator-Apodem	Pe	Penis
Ed	Epithel, drüsig differenziert	pG	primärer Gonoporus
Ep	Endophallus	Pgp	Postgenitalplatte
Epi	Epidermis	Pgr	Pleuralgrube
Epm	Epimerum	PlA	Platten-Apodem
EpPl	Endophallus-Platte	Pph	Postphragma
Es I,III	Episternum I,III	Po	Polster
		Ppn	Postpronotum
Fe	Femur	Pt	Phallotrema
Fl	Flügel-Ansatz	Pu	Pumpenraum
G	Gonocoxit	PuVo	Pumpenvorraum
GA	Gonocoxit-Apodem	Pz	Palisadendrüsenzelle
GF	Gonocoxit-Fortsatz	R	Rectum

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S I-IX	Sternum I-IX		Tbgr	Tibialgrube
Sc	Scutum		Tbsp	Tibialsporn
Scu	Scutellum			
Sk	Sekret		Vbg	Verbindungsgang
Sp	Sperma		Vd	Vas deferens
Spe	Spermatophore		Ve	Vesicula seminalis
Spg	Spermagang		Vesk	Ventilsklerit
Sppu	Spermapumpe		vL	ventrale Lamelle
Spr	Spermareservoir		vLe	ventrale Leiste
Spth	Spermatheca		vM	ventrale Membran
SpthD	Ductus Spermathecae		vPl	ventrale Platte
St VIII	Stigma VIII		Vsk	Ventralsklerit
T I-X	Tergum I-X		vSp	ventrale Spange
Ta	Tarsus			
Tb	Tibia		Zk	Zähnchenkamm

Anschrift der Verfasserin:
Dr. Ute Blaschke-Berthold, Bergstraße 10, D-41849 Wassenberg
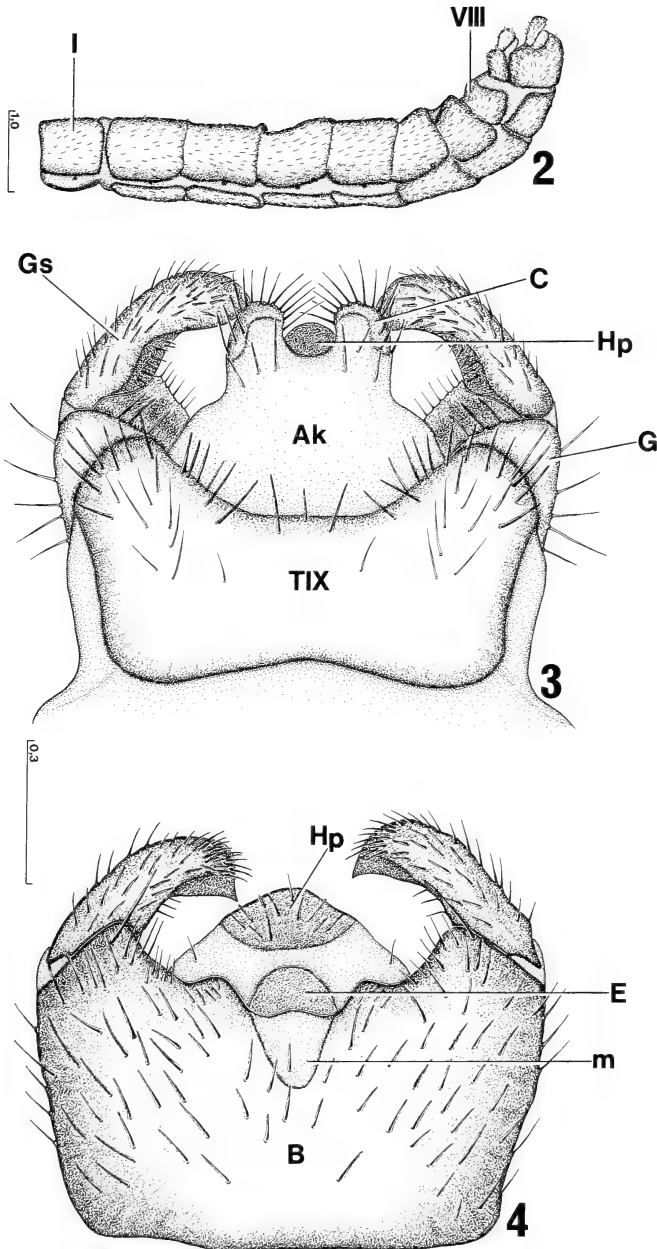
Fig.2-4: *Penthetria funebris* ♂: (2) Abdomen, von lateral; (3) Terminalkomplex, von dorsal; (4) Terminalkomplex, von ventral. Maßstäbe in mm.

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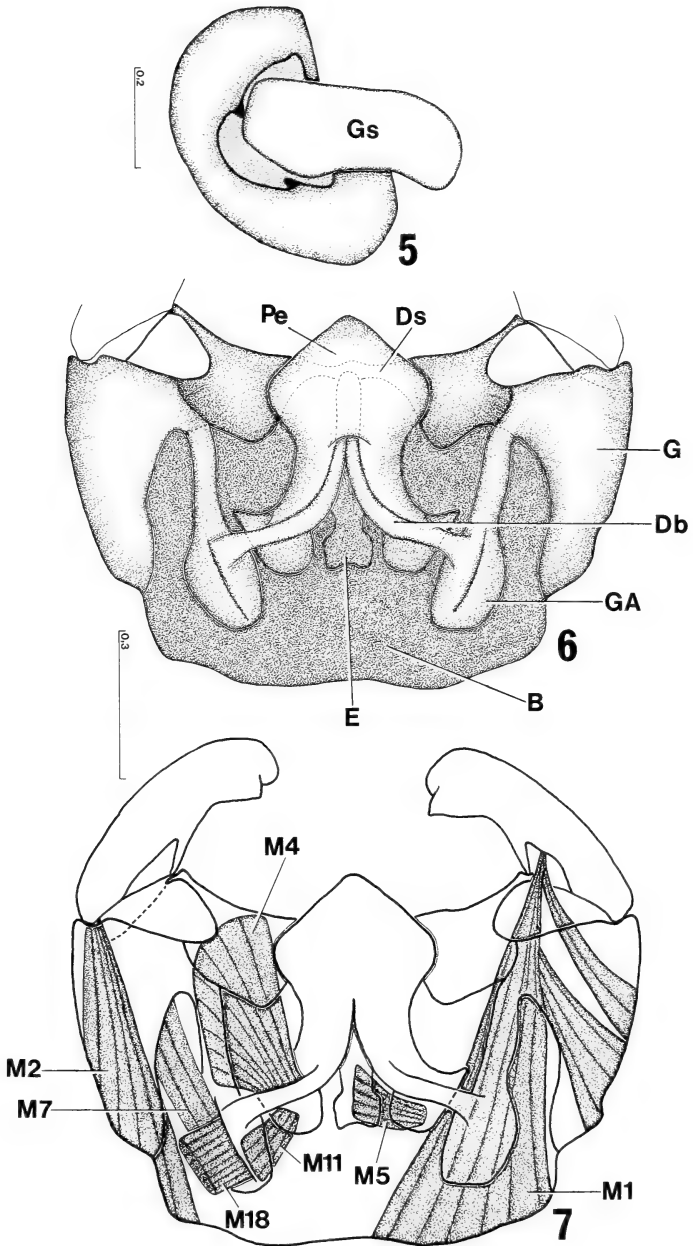
Fig.5-7: *P. funebris* ♂: (5) Gelenkung zwischen Gonocoxit und Gonostylus; (6) ventrale Teile des Genitalsegments mit Penis, von dorsal; (7) dieselben Teile mit Muskulatur, von dorsal. Maßstäbe in mm.
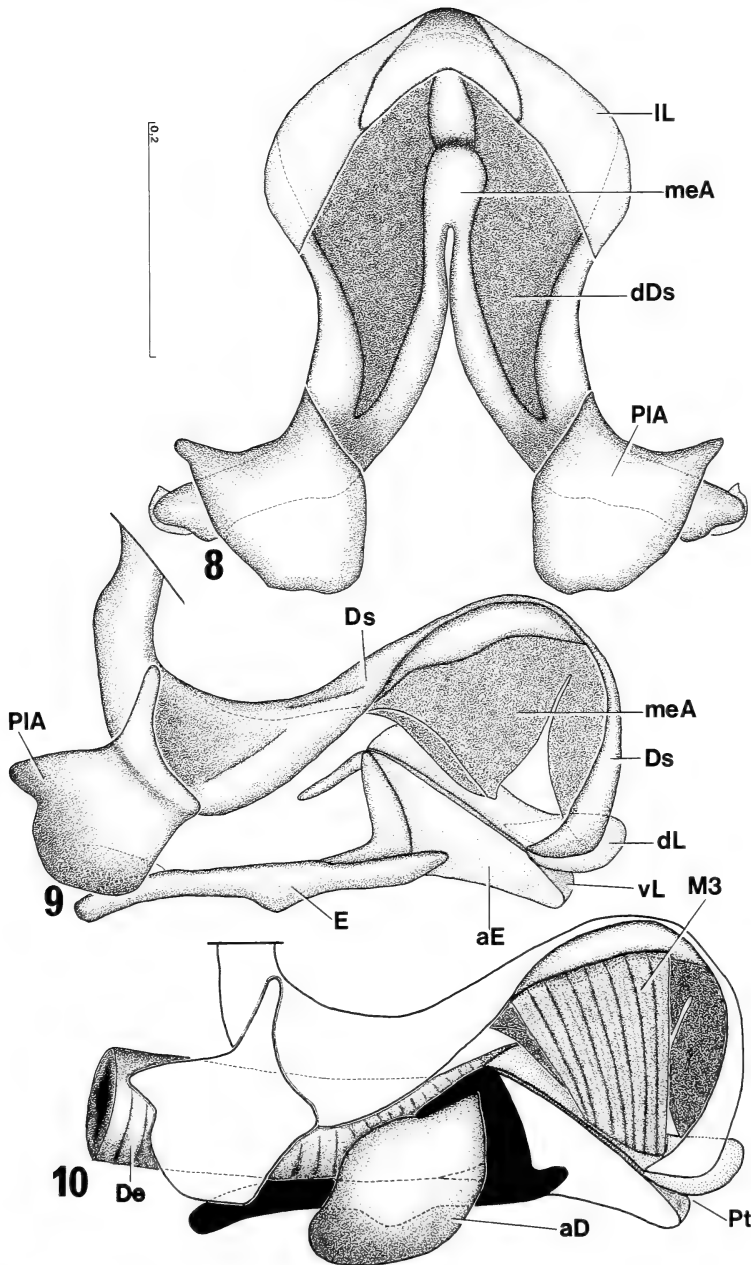
Fig.8-10: Penis von *P. funebris*: (8) Dorsalsklerit, von ventral; (9) Dorsalsklerit und Ejaculator-Apodem, von lateral; (10) Weichteile des Penis: Ductus ejaculatorius und akzessorische Drüse. Maßstab in mm.

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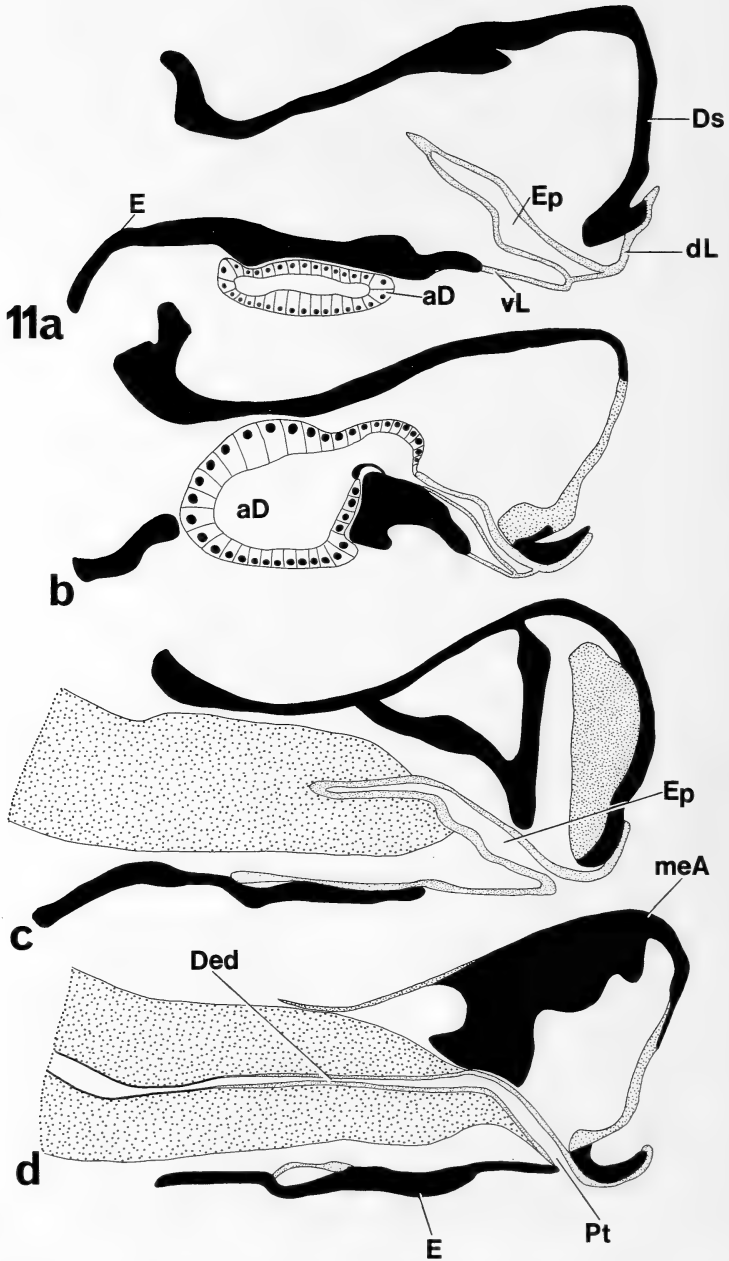
Fig.11a-d: Penis von *P. funebris*, sagittal (schematisch): (a, b) Mündung der akzessorischen Drüse in den Endophallus; (c, d) Mündung des Ductus ejaculatorius in den Endophallus.
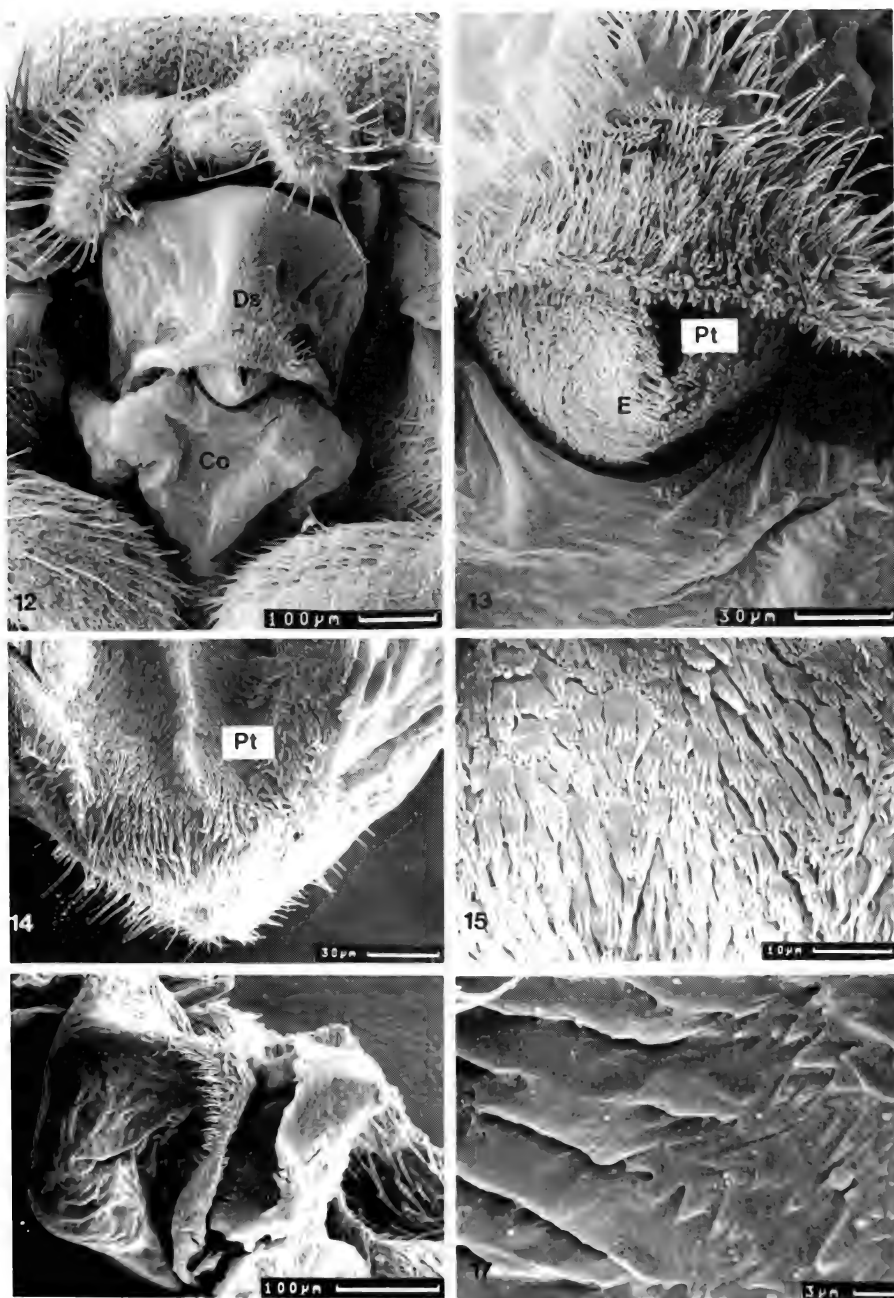
Fig.12-17: Penis von *P. funebris*, REM: (12, 13) von frontal, das unpaare Phallotrema (Pt) ist zu erkennen. (14, 15) Dorsalseite des Endophallus, von innen. (16) Penis mit Spermatophore (vgl. Fig.70); sie bleibt während der Kopulation mit dem Penis verbunden. (17) Oberfläche der Spermatophore.
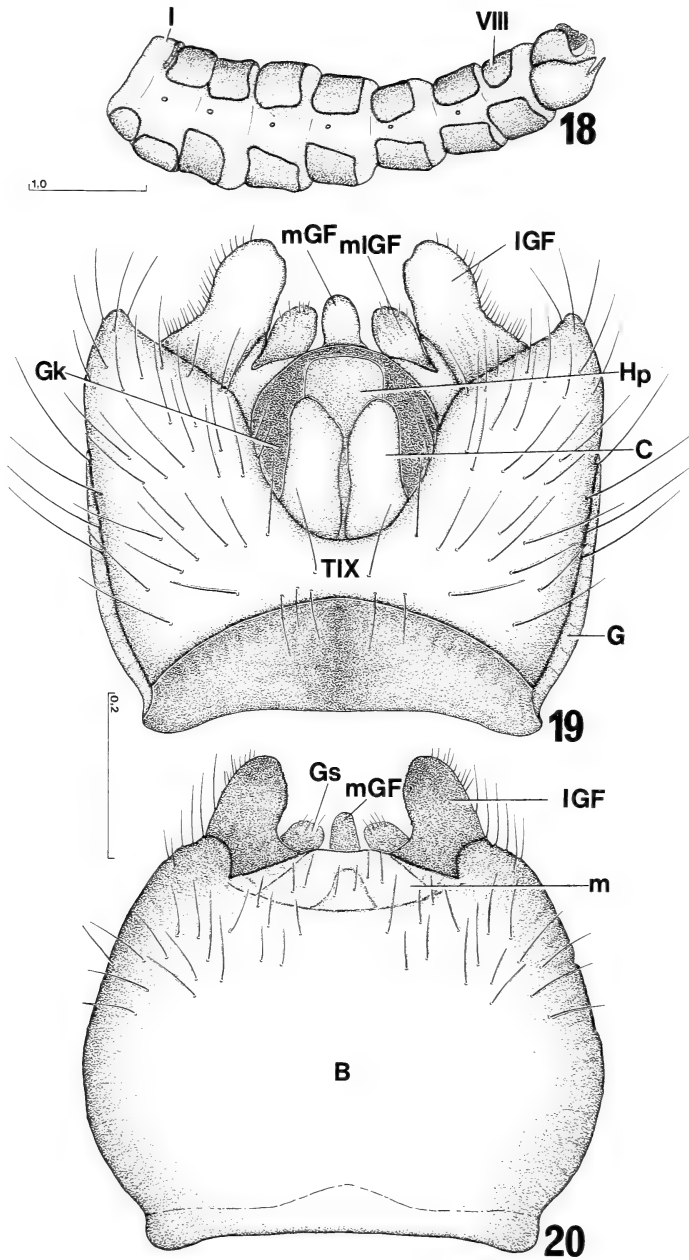
Fig.18-20: *Plecia ornaticornis* ♂: (18) Abdomen, von lateral; (19) Terminalkomplex, von dorsal; (20) Terminalkomplex, von ventral. Maßstäbe in mm.
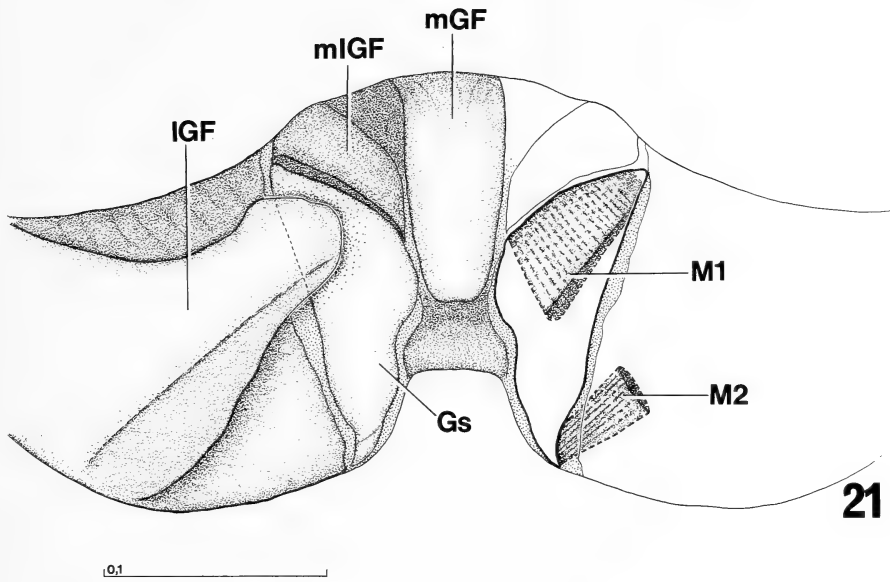
Fig.21: *P. ornaticornis* ♂: Terminalia, von frontal; die kleinen Gonostyli (Gs) sind medial verschoben. Maßstab in mm.
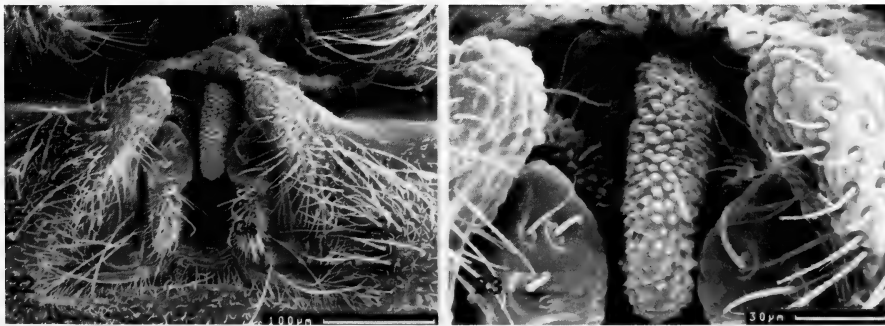
Fig.22-23: *P. ornaticornis* ♂: Terminalia, von frontal (REM); (22) Übersicht und (23) Cuticula, Detail.

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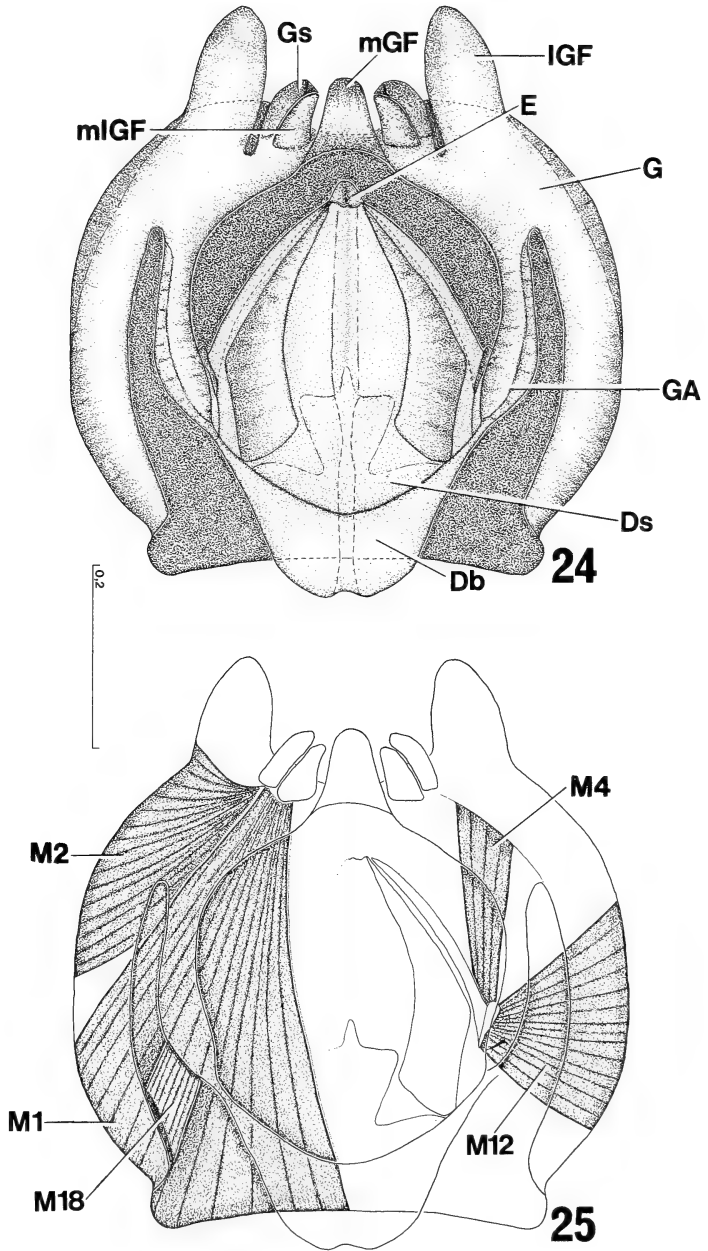
Fig.24-25: *P. ornaticornis* ♂: (24) ventrale Teile des Genitalsegments mit Penis, von dorsal; (25) dieselben Teile mit Muskulatur, von dorsal. Maßstab in mm.
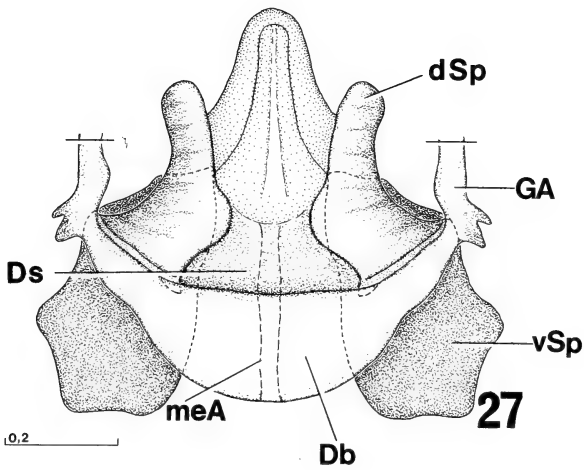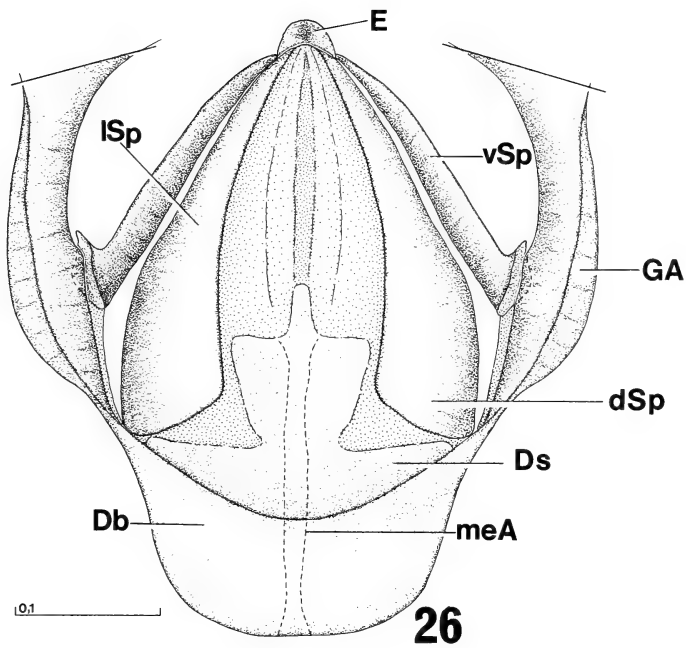
Fig.26-27: Dorsalsklerit des Penis und seine Verbindung mit den Gonocoxit-Apodemen: (26) *P. ornaticornis*, (27) *P. amplipennis*. Maßstab in mm.
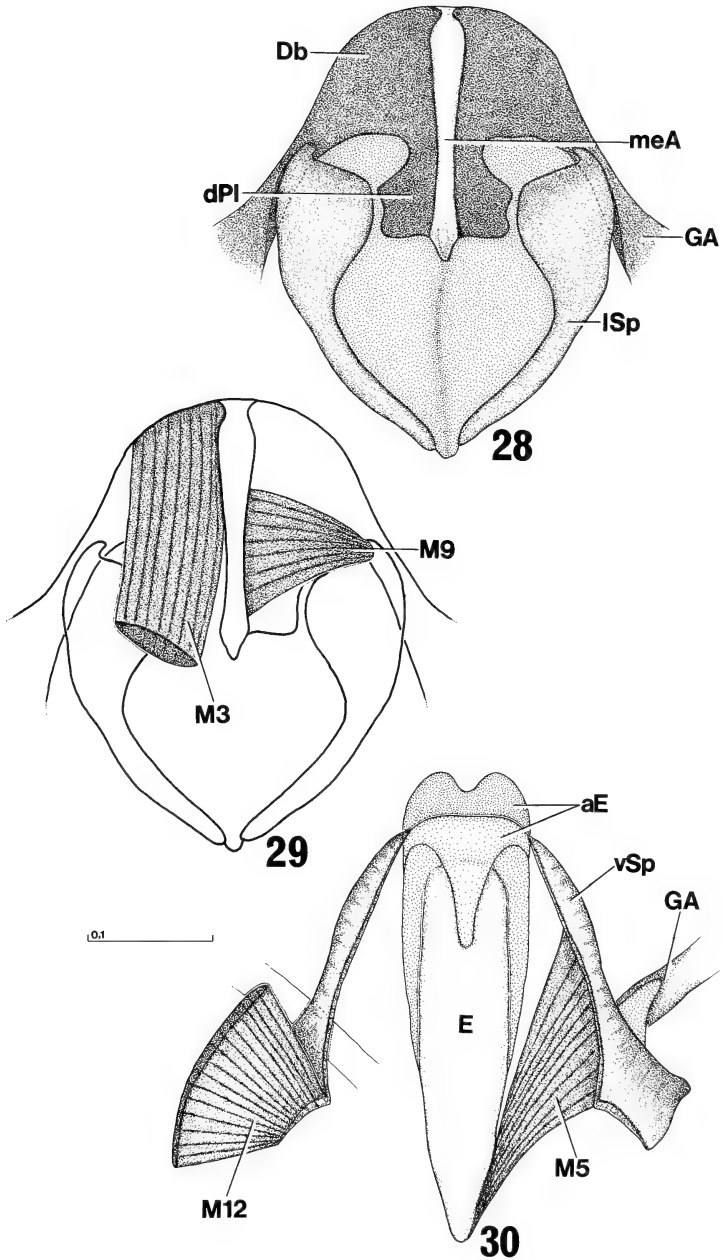
Fig.28-30: Penis von *P. ornaticornis*: (28) Dorsalsklerit, von innen; (29) Dorsalsklerit mit Muskulatur, von innen; (30) Ejaculator-Apodem mit Muskulatur, von ventral. Maßstab in mm.
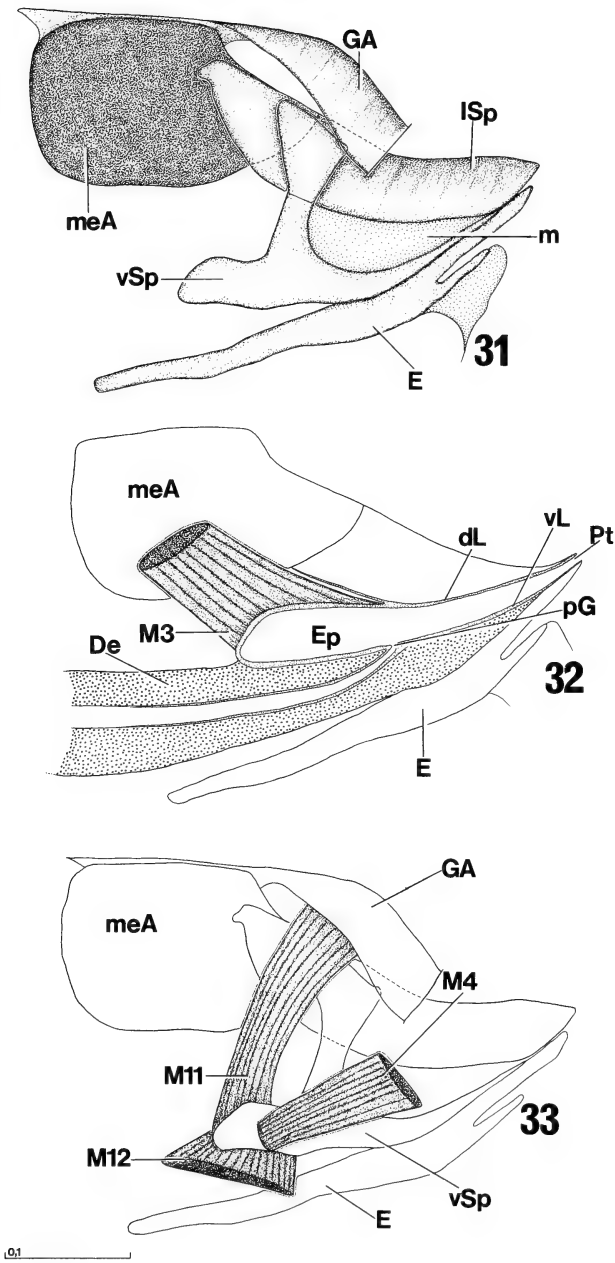
Fig.31-33: Penis von *P. ornaticornis*: (31) sklerotisierte Elemente, von lateral; (32) medio-sagittal; (33) Muskulatur, von lateral. Maßstab in mm.

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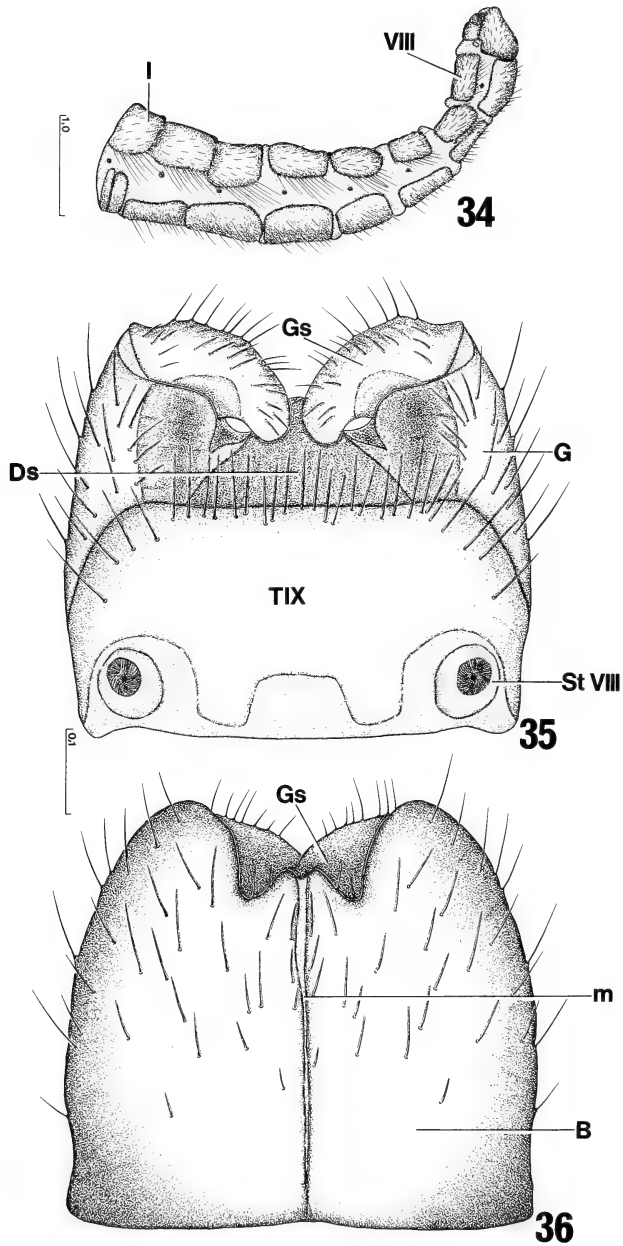
Fig.34-36: *Dilophus febrilis* ♂: (34) Abdomen, von lateral; (35) Terminalkomplex, von dorsal; beachtenswert ist die Lage der Stigmen (St VIII); (36) Terminalkomplex, von ventral. Maßstäbe in mm.
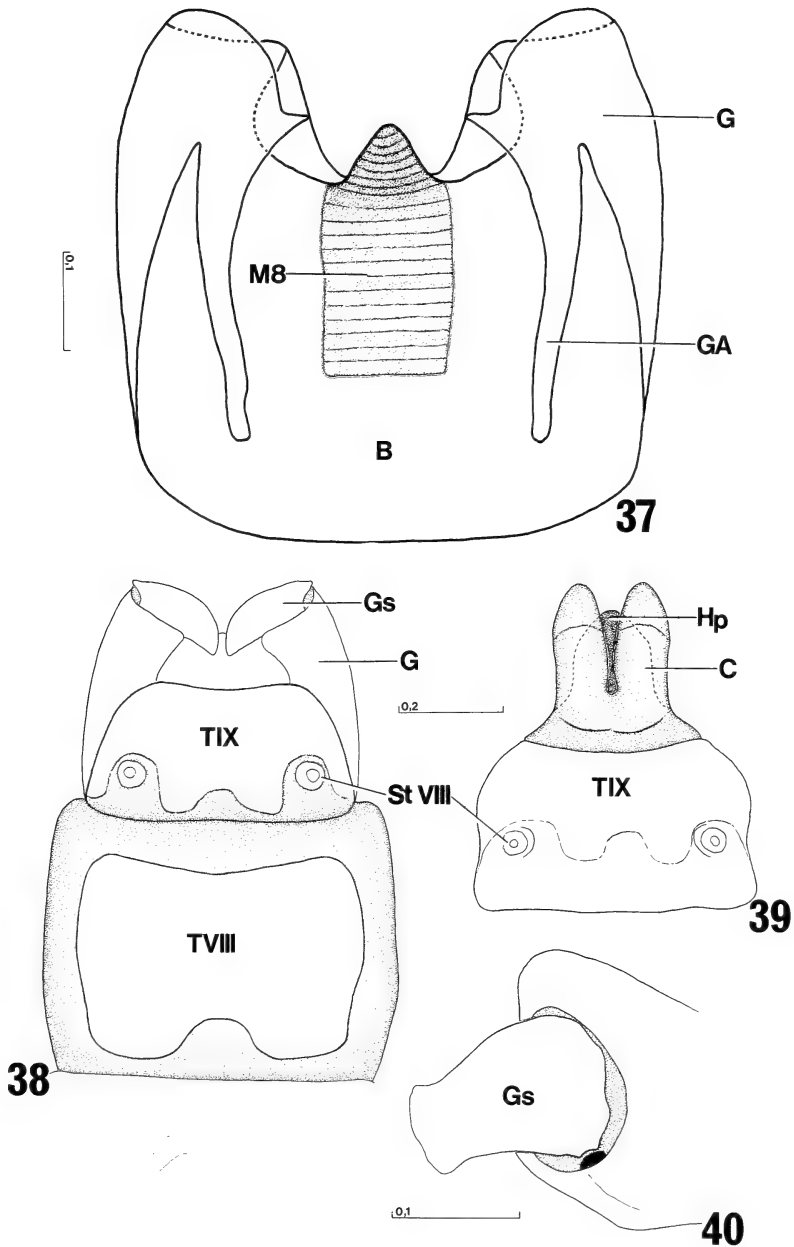
Fig.37-40: *D. febrilis* ♂: (37) Muskulatur des Genitalsegment-Bodens; (38) Lage des letzten Stig-menpaares im Bereich des Tergum IX; (39) Analkomplex, von dorsal; (40) Gelenkung zwischen Gonocoxit und Gonostylus. Maßstäbe in mm.

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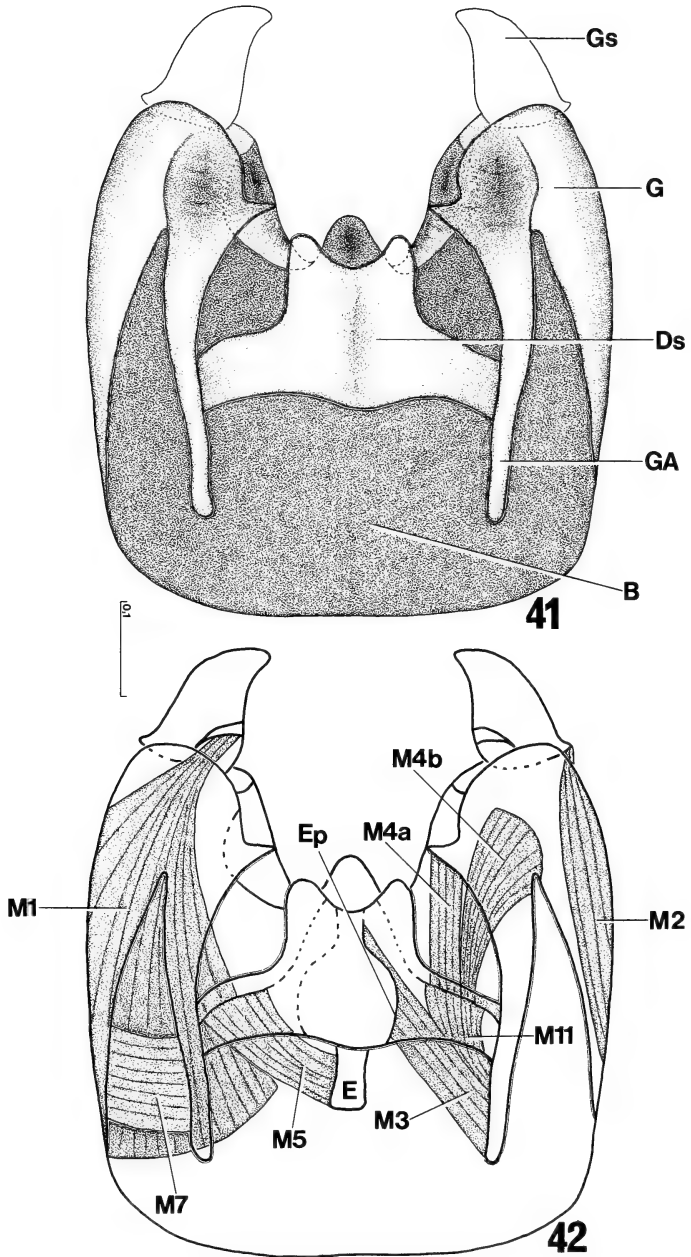
Fig.41-42: *D. febrilis* ♂: (41) ventrale Teile des Genitalsegments mit Penis, von dorsal; (42) dieselben Teile mit Muskulatur, von dorsal. Maßstab in mm.
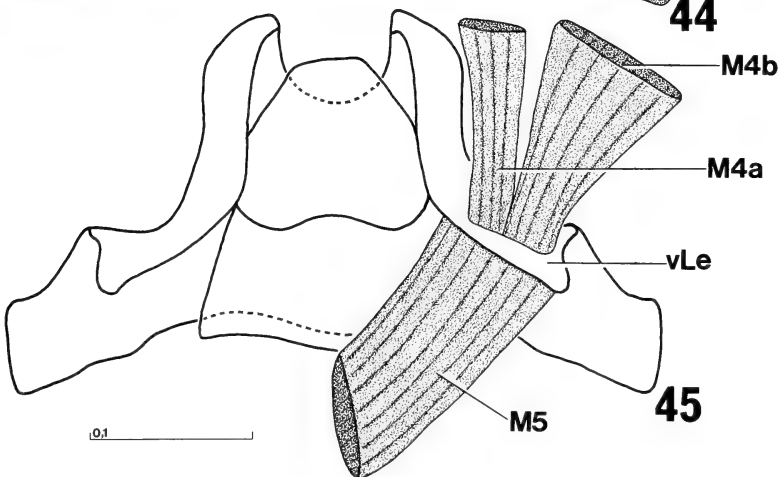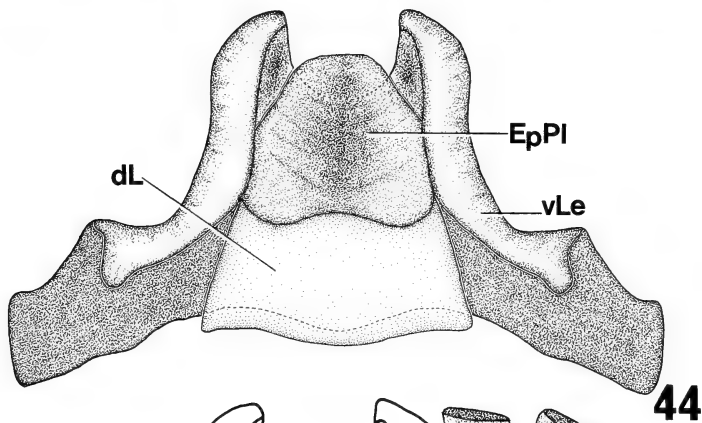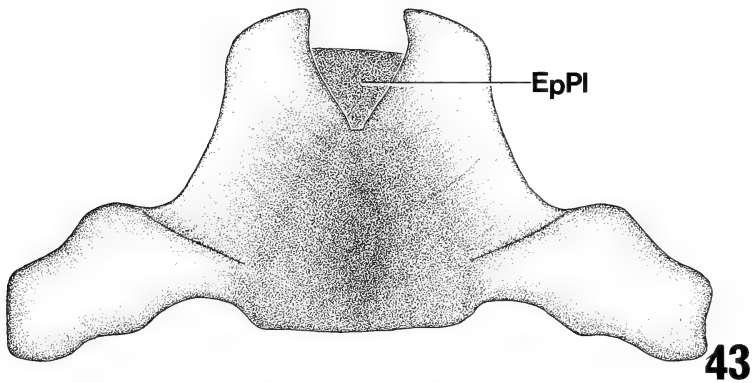
Fig.43-45: Penis von *D. febrilis*: (43) Dorsalsklerit, von dorsal; (44) Dorsalsklerit, von ventral; (45) Muskulatur des Dorsalsklerits, von ventral. Maßstab in mm.

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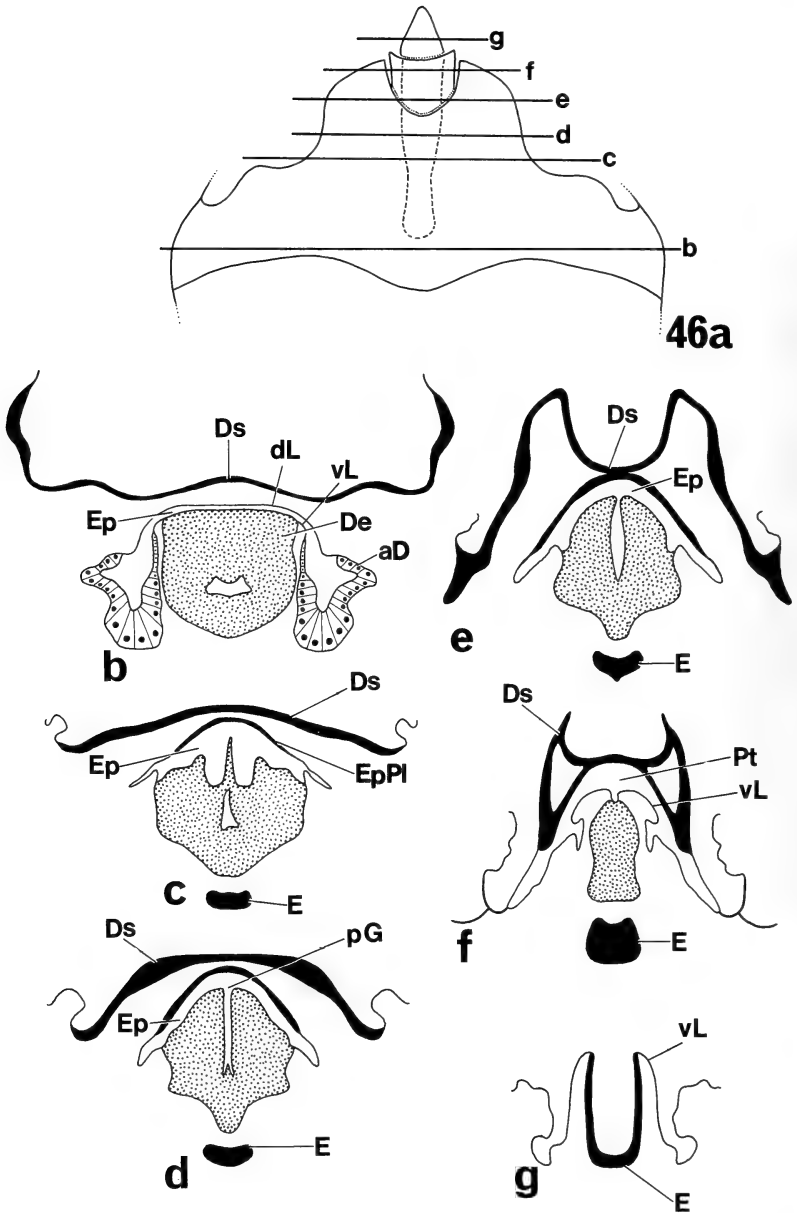
Fig.46a-g: Penis von *D. febrilis*, quer (schematisch): (a) Schnittführung; (b) Mündung der akzesso-rischen Drüse in den Endophallus; (c,d) Mündung des Ductus ejaculatorius in den Endophallus; (e) Verbindung des Endophallus mit der Innenseite des Dorsalsklerits; (f,g) Bereich des Phallo-trema.
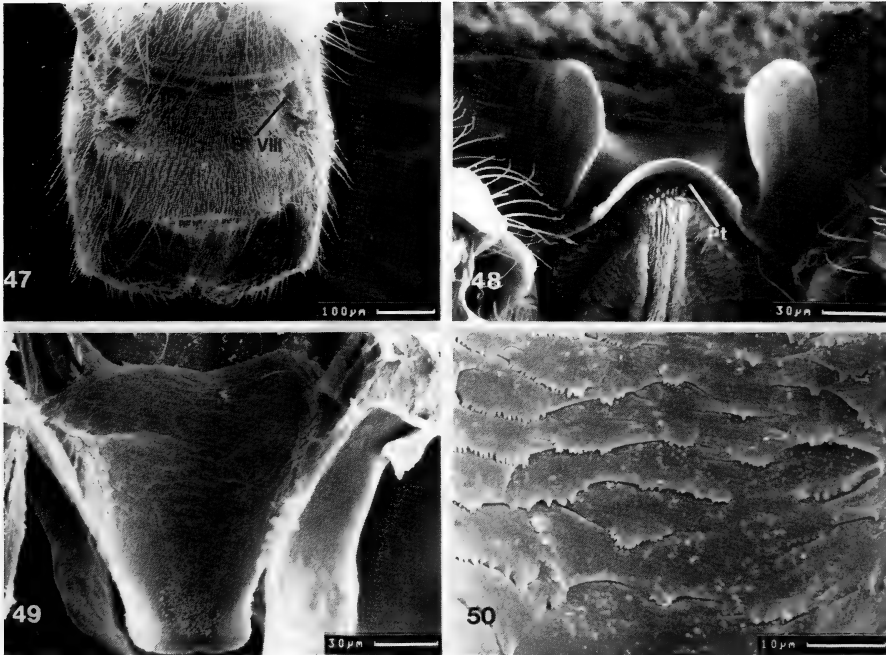
Fig.47-50: *D. febrilis* ♂, REM: (47) Terminalkomplex, von dorsal; (48) Penis, von frontal (vgl. Fig.46f); (49) Dorsalfläche des Endophallus, von innen; (50) Detail von (49), Schuppenhaare.

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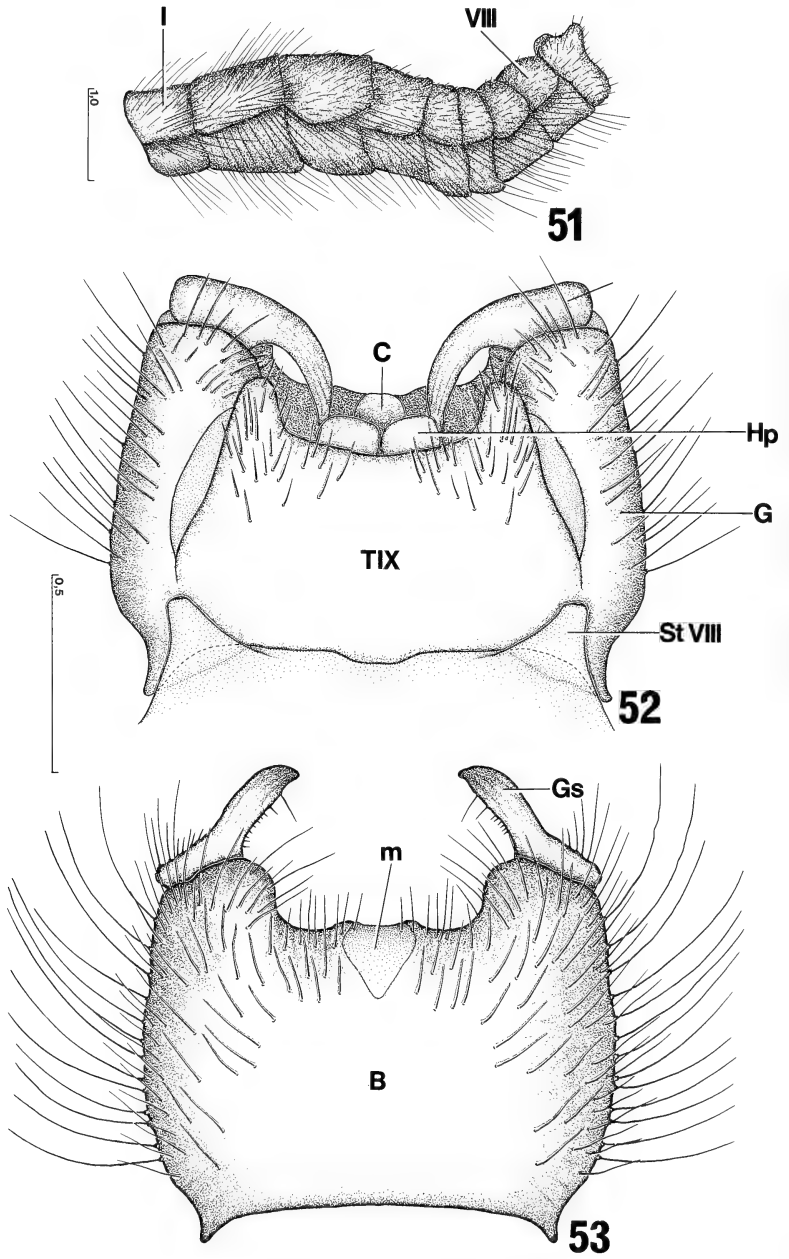
Fig.51-53: *Bibio marci* ♂: (51) Abdomen, von lateral; (52) Terminalia, von dorsal; (53) Terminalia, von ventral. Maßstäbe in mm.
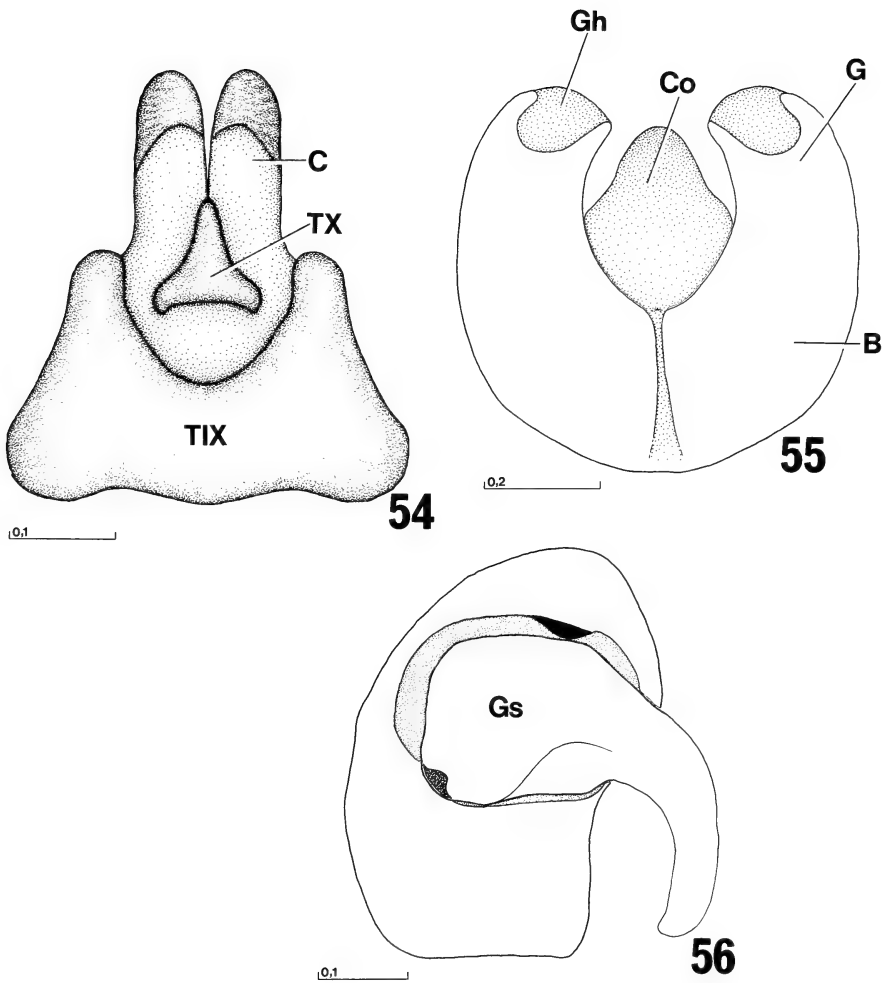
Fig.54-56: *B. leucopterus* ♂: (54) Analkomplex, ausgestülpt; (55) Gonocoxite, von ventral; (56) Gelenkung zwischen Gonocoxit und Gonostylus. Maßstäbe in mm.
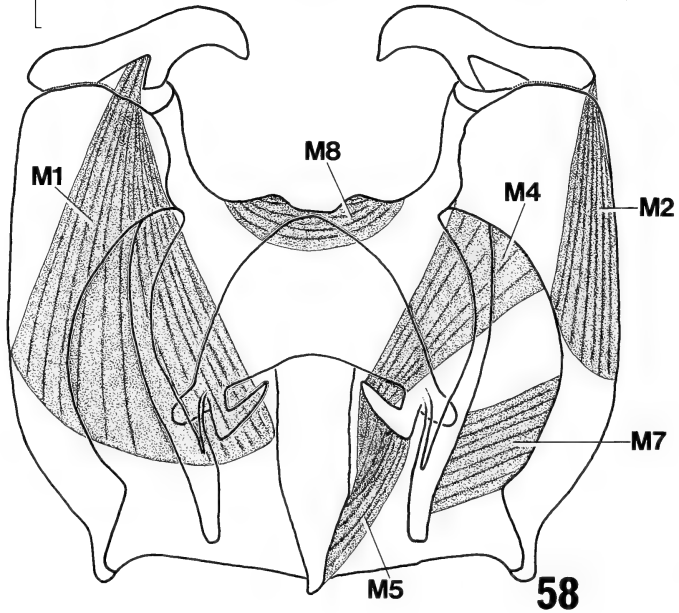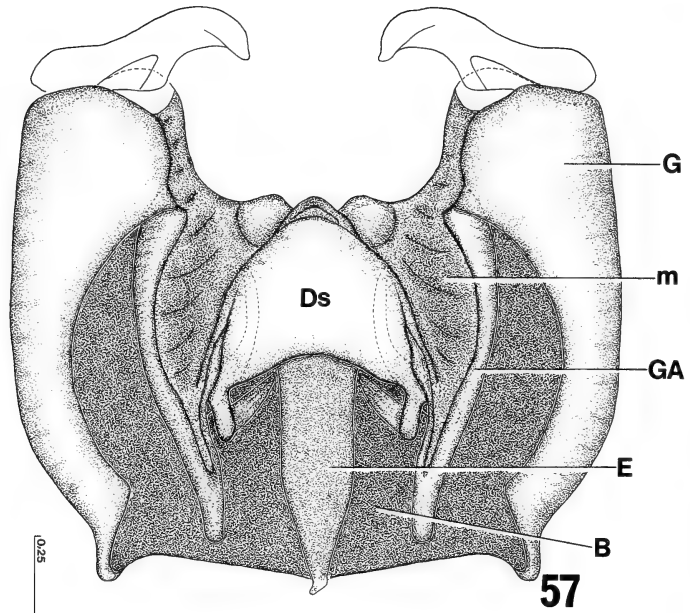
Fig.57-58: *B. marci* ♂: (57) ventrale Teile des Genitalsegments mit Penis, von dorsal; (58) dieselben Teile mit Muskulatur, Dorsalansicht. Maßstab in mm.
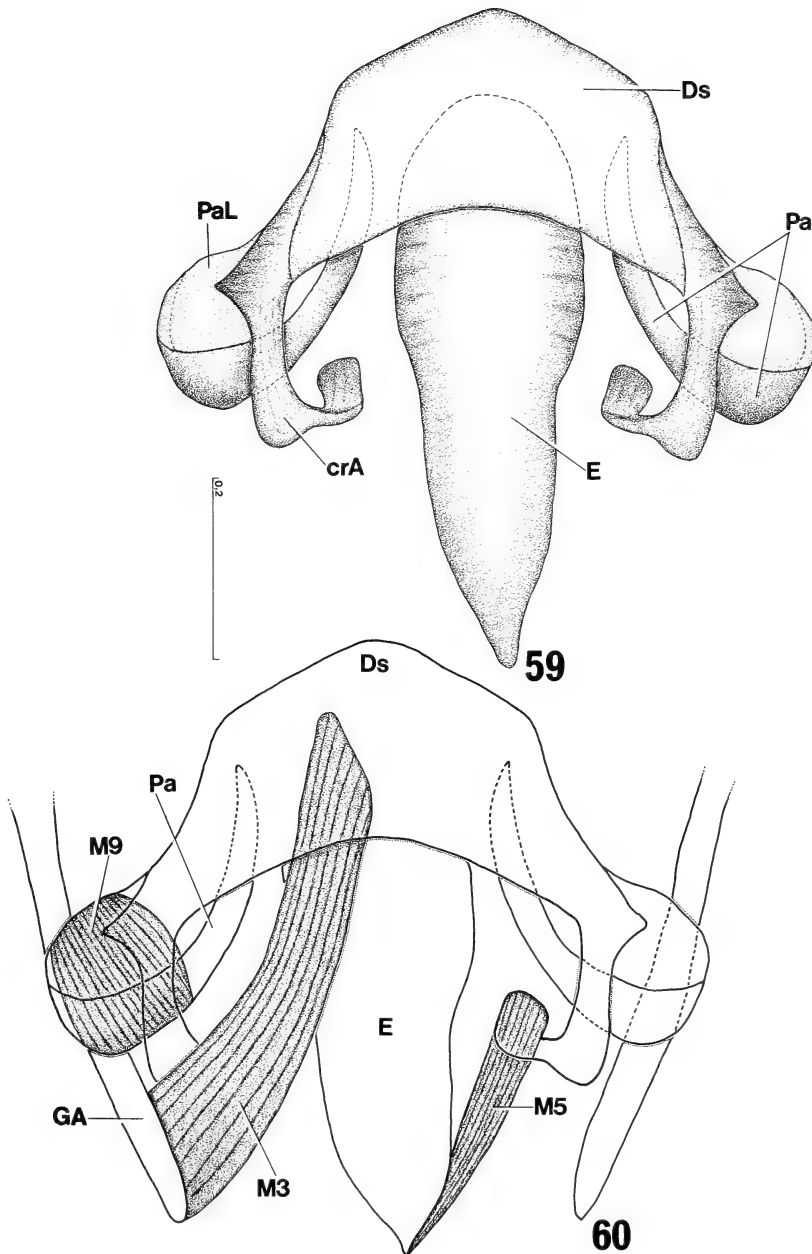
Fig.59-60: Penis von *B. marci*: (59) Dorsalsklerit und Ejaculator-Apodem; (60) Muskulatur, von dorsal. Maßstab in mm.
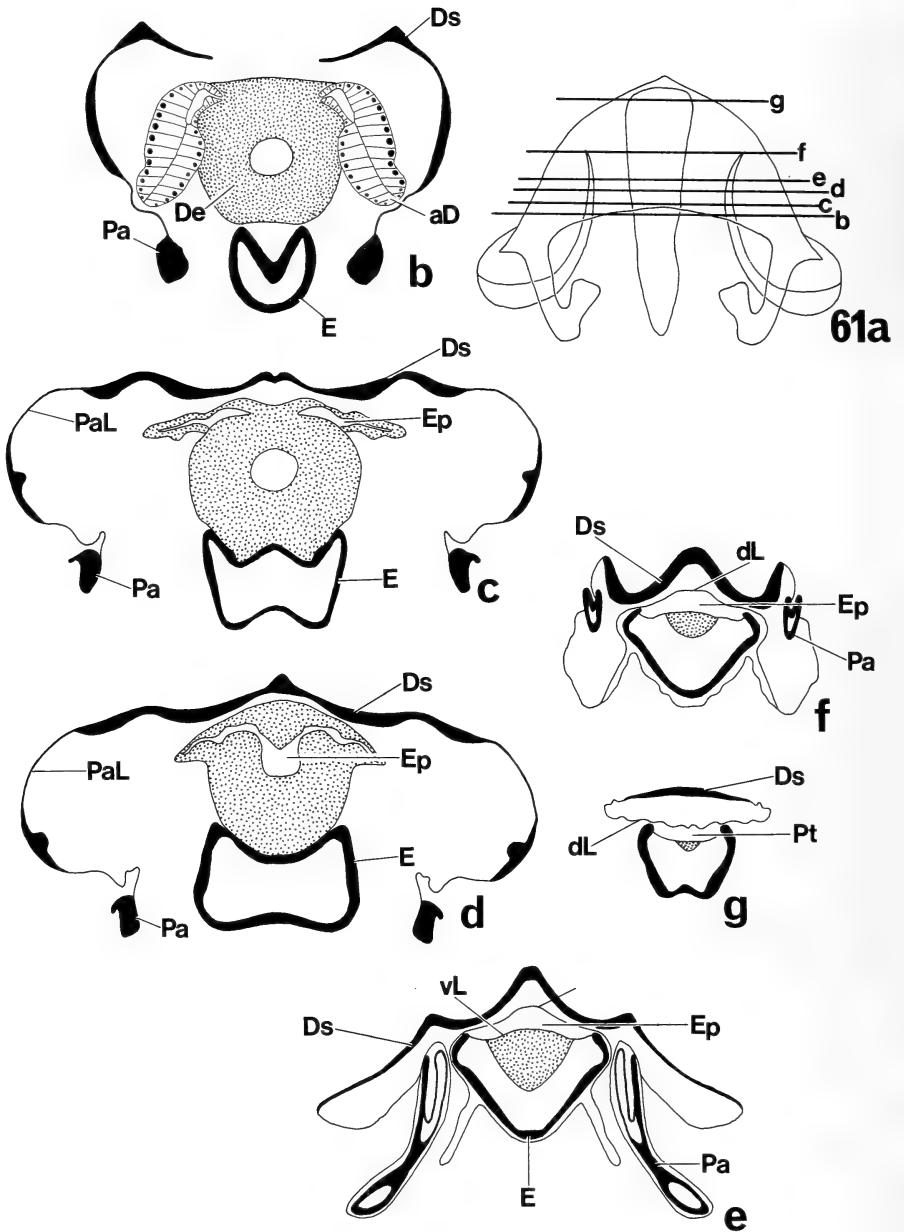
Fig.61a-e: Penis von *B marci*, quer (schematisch): (a) Schnittführung; (b,c) Mündung der akzessorischen Drüse in den Endophallus; (d,e) Mündung des Ductus ejaculatorius in den Endophallus; (f) apikaler Bereich des Endophallus; (g) Bereich des Phallotrema.
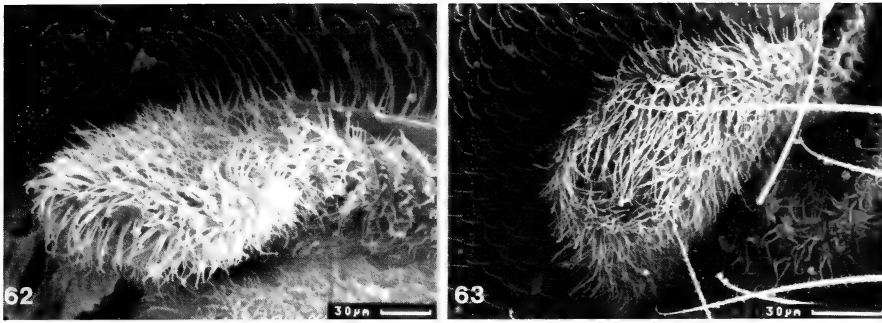
Fig.62-63: 8. abdominales Stigmenpaar (REM) des ♂ von (62) *B. marci* und (63) *B. leucopterus*.
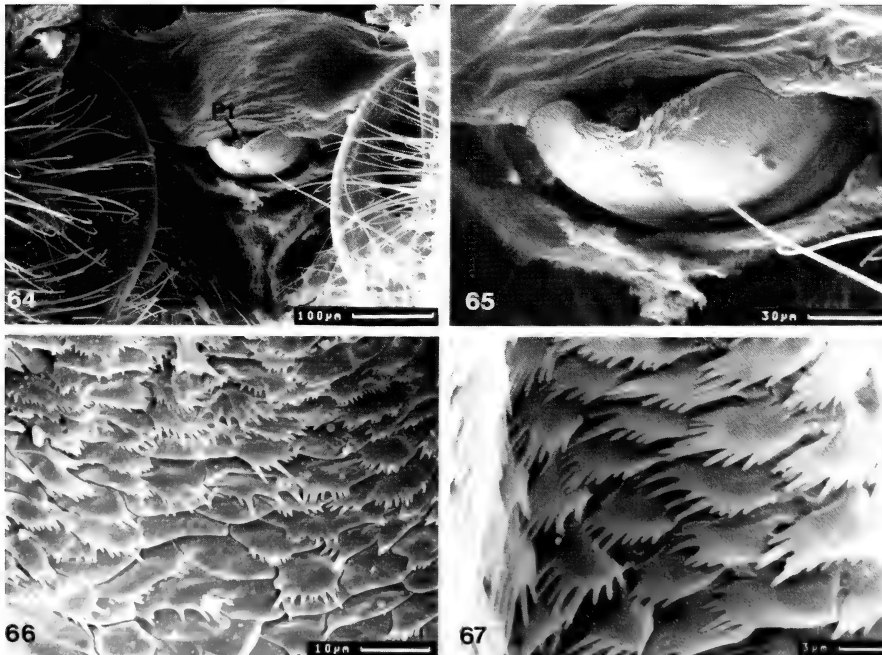
Fig 64-67: Penis von *B. marci*, REM: (64) Lage des Penis zwischen den Gonocoxiten, von frontal; (65) Detail von (64), unpaares Phallotrema; (66) Dorsalfläche des Endophallus, von innen; (67) Dorsalfläche des Endophallus im Bereich des Phallotrema, von innen.
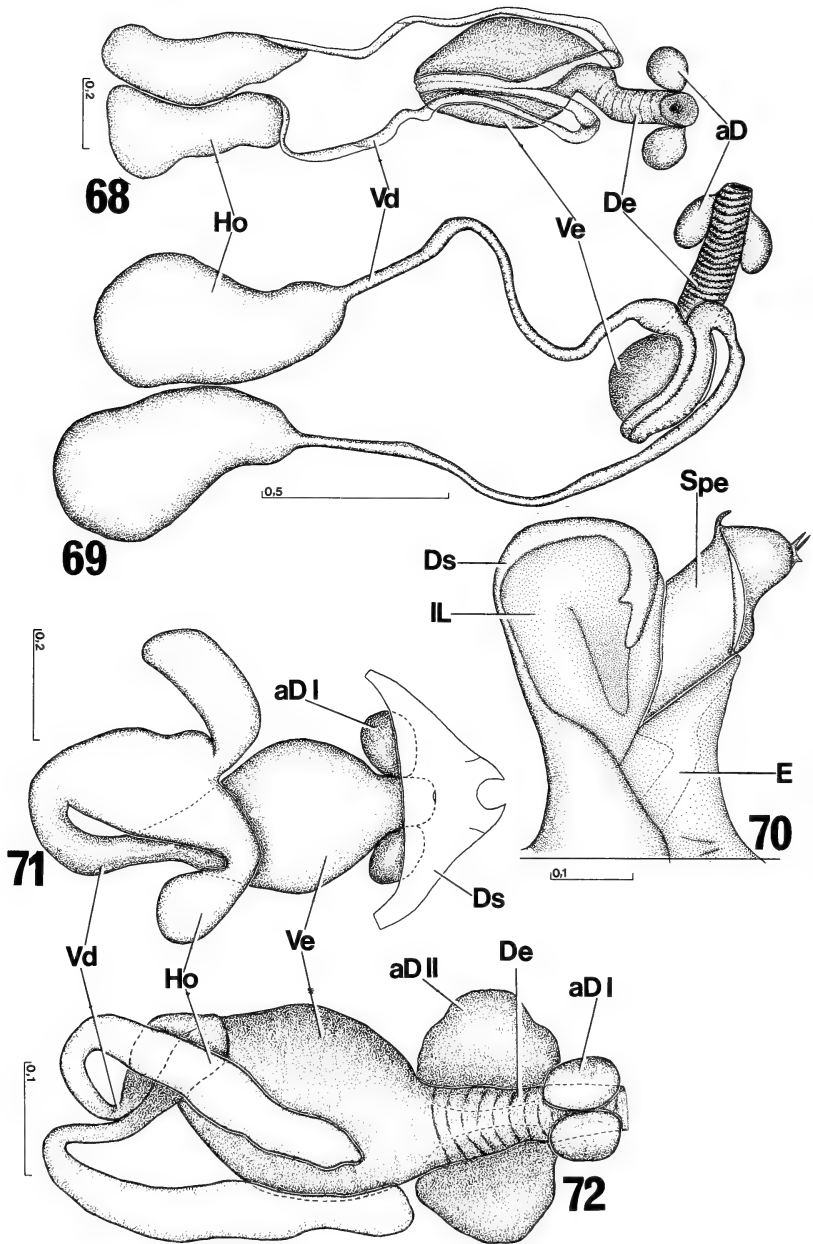
Fig.68-72: Innere Geschlechtsorgane und Anhangsdrüsen der ♂ von (68) *Plecia ornaticornis*, (69,70) *Penthetria funebris*, (71) *Dilophus febrilis* und (72) *Bibio marci*.
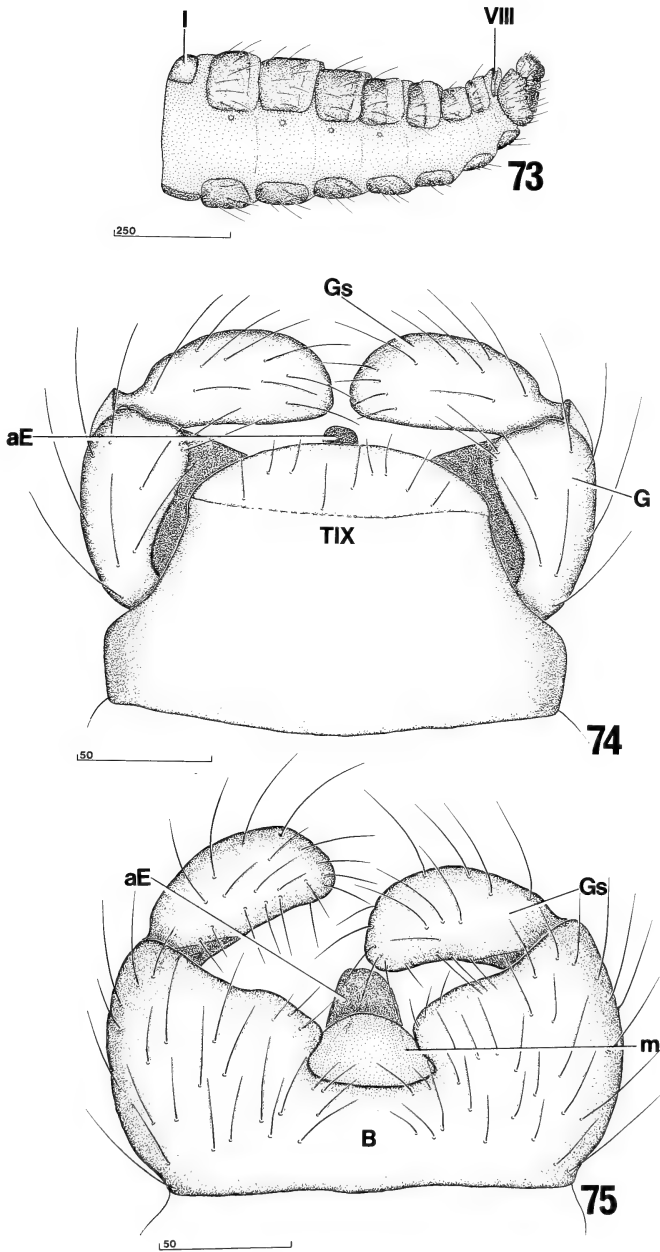
Fig.73-75: *Campylomyza flavipes* ♂: Abdomen, (73) Lateralansicht; (74) Terminalkomplex, von dorsal; (75) Terminalia, von ventral. Maßstäbe in μm.
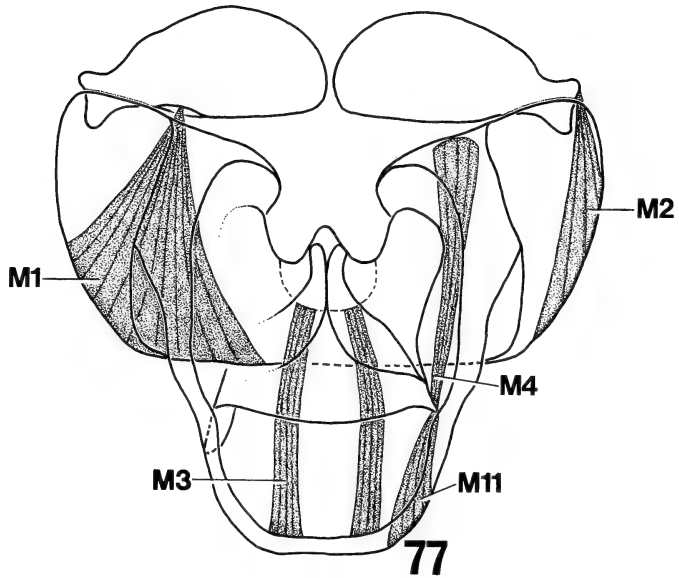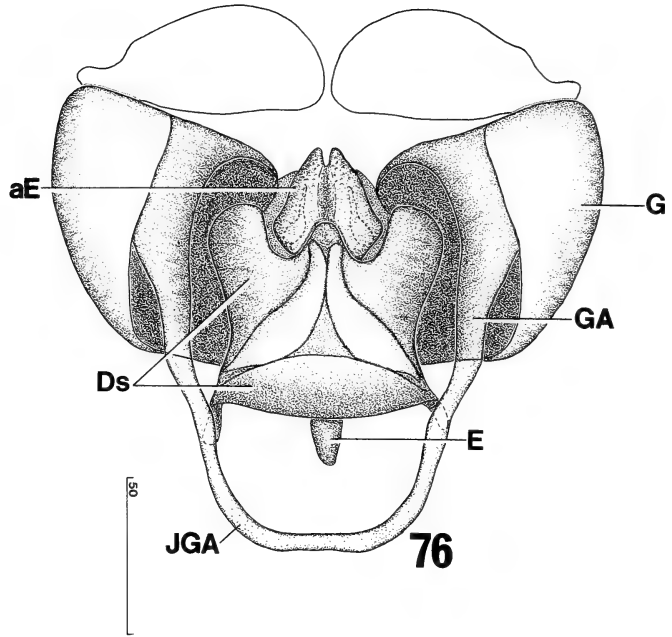
Fig.76-77: *C. flavipes* ♂: (76) ventrale Teile des Genitalsegments mit Penis, von dorsal; (77) dieselben Teile mit Muskulatur, von dorsal. Maßstab in μm.
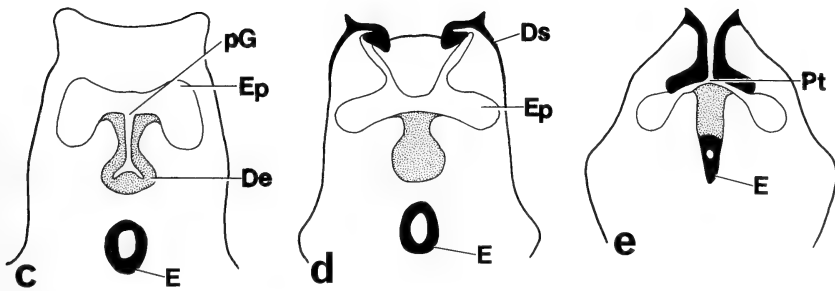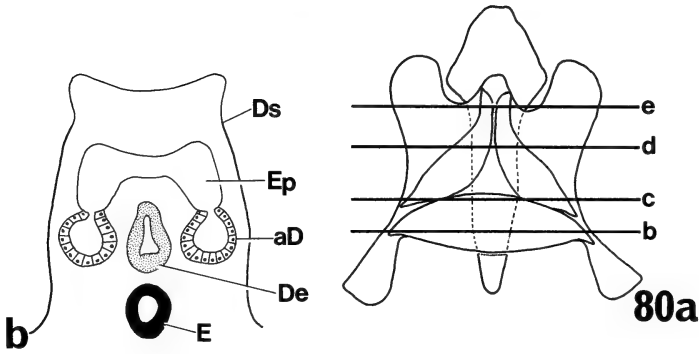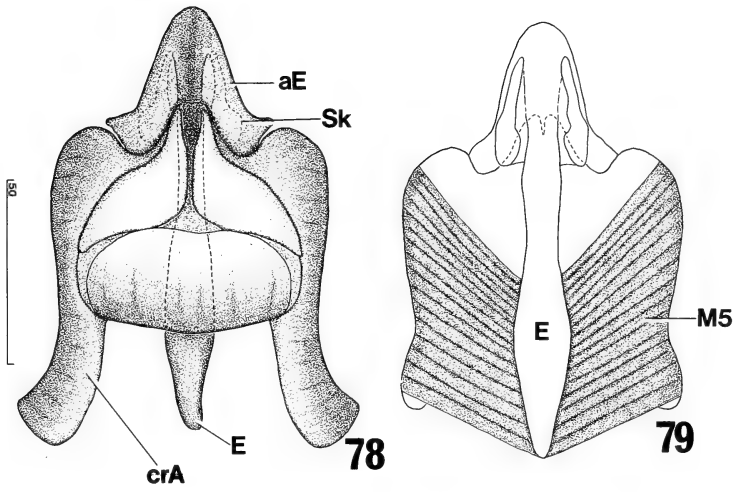
Fig.78-80: Penis von *C. flavipes*: (78) sklerotisierte Elemente, von dorsal; (79) Ejaculator-Apodem mit Muskulatur, von ventral; Maßstab in µm. (80a-e) Penis, quer (schematisch): (a) Schnittführung; (b) Mündung der akzessorischen Drüsen in den Endophallus; (c) Mündung des Ductus ejaculatorius in den Endophallus; (d) Befestigung des Endophallus am Dorsalsklerit; (e) Bereich den Phallotrema.

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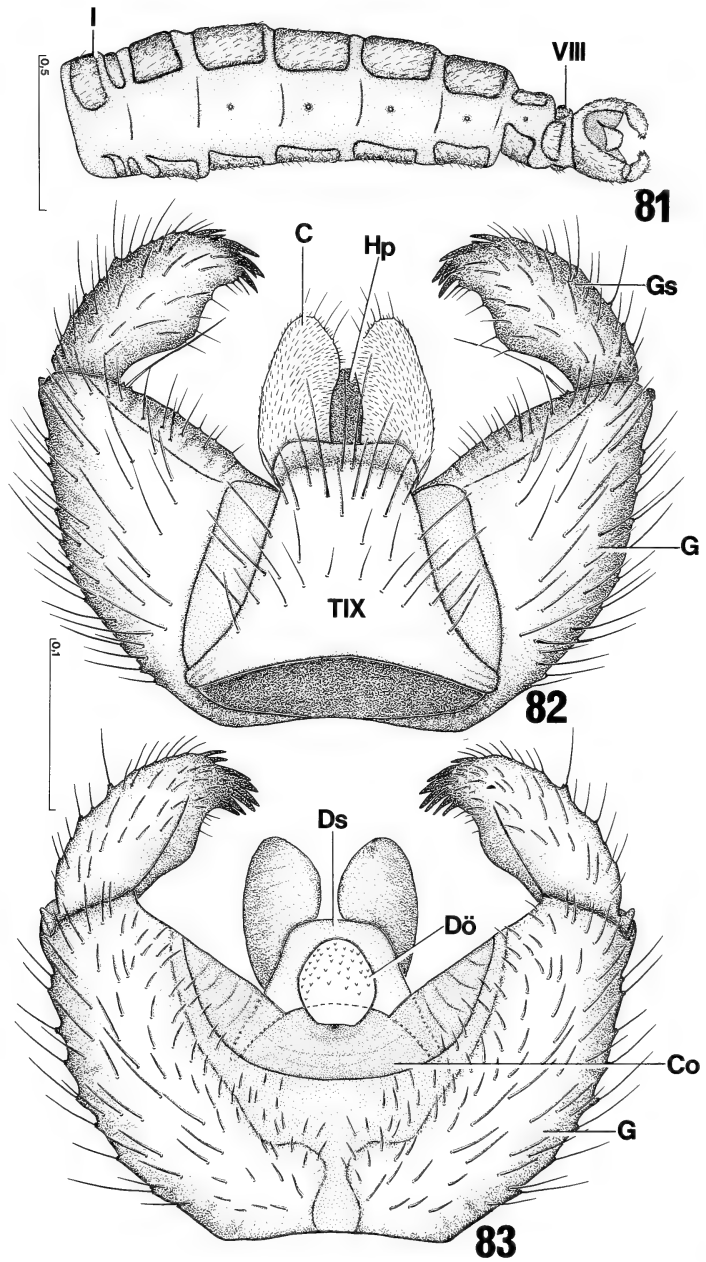
Fig.81-83: *Bradysia amoena* ♂: (81) Abdomen, von lateral; (82) Terminalkomplex, Dorsalansicht; (83) Terminalkomplex, Ventralansicht. Maßstäbe in mm.
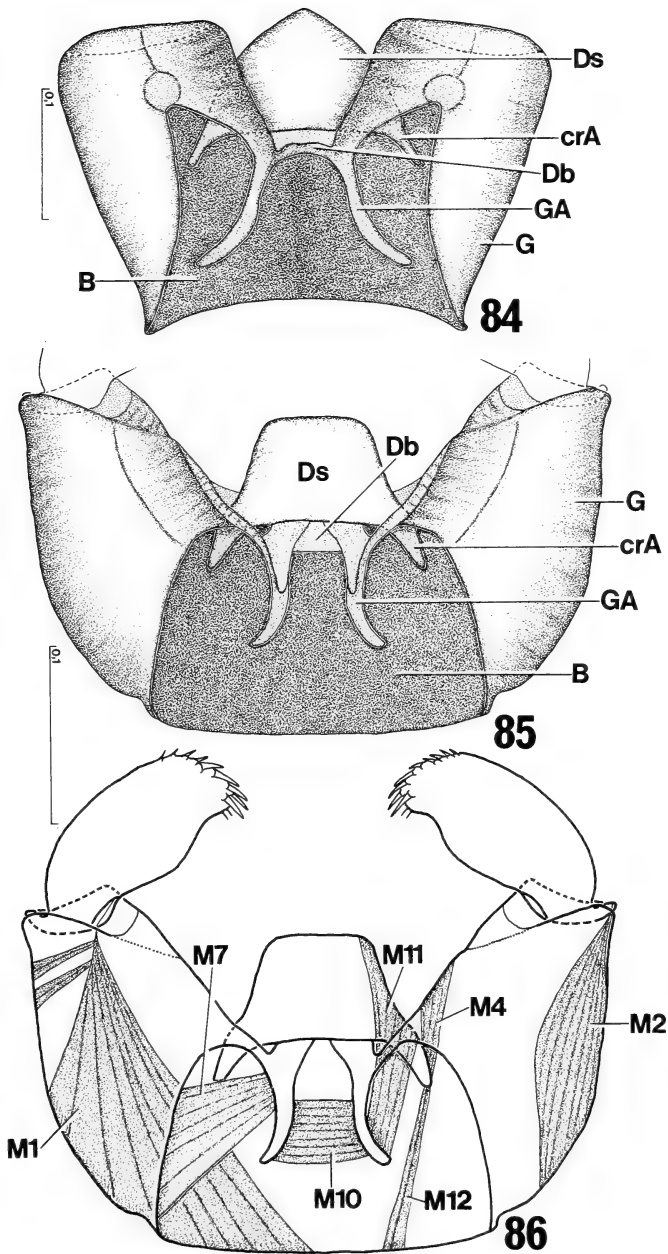
Fig.84-86: ventrale Teile des Genitalsegments mit Penis von (84) *Trichosia trochanterata*, Exoskelett; (85) *Bradysia amoena*, Exoskelett; (86) *B. amoena*, Muskulatur. Maßstäbe in mm.
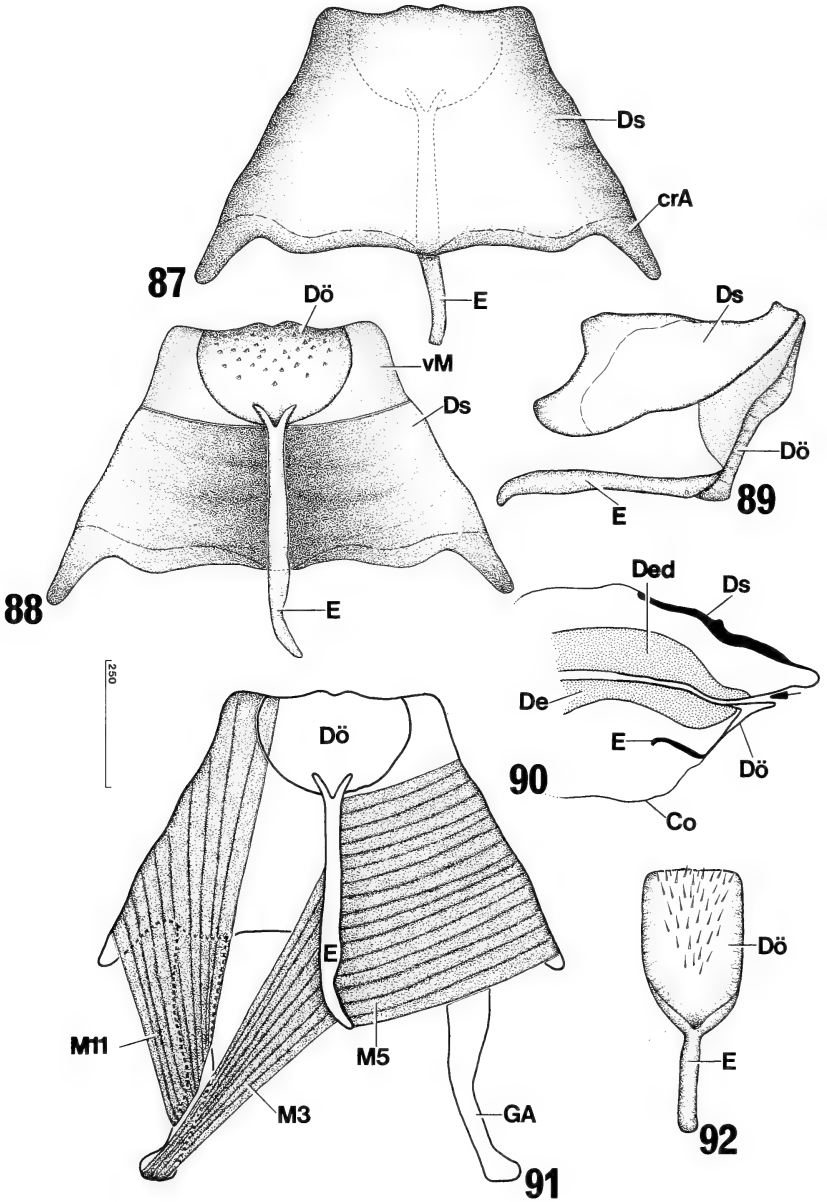
Fig.87-92: Penis von *B. amoena*: (87) Dorsalsklerit und Ejaculator-Apodem, von dorsal; (88) Dorsalsklerit und Ejaculator-Apodem, von ventral; (89) sklerotisierte Elemente, Lateralansicht; (90) Penis, medio-sagittal; (91) Penis-Muskulatur, von ventral; (92) Ejaculator-Apodem und Dörnchenplatte von *Trichosia trochanterata*. Maßstab in μm.
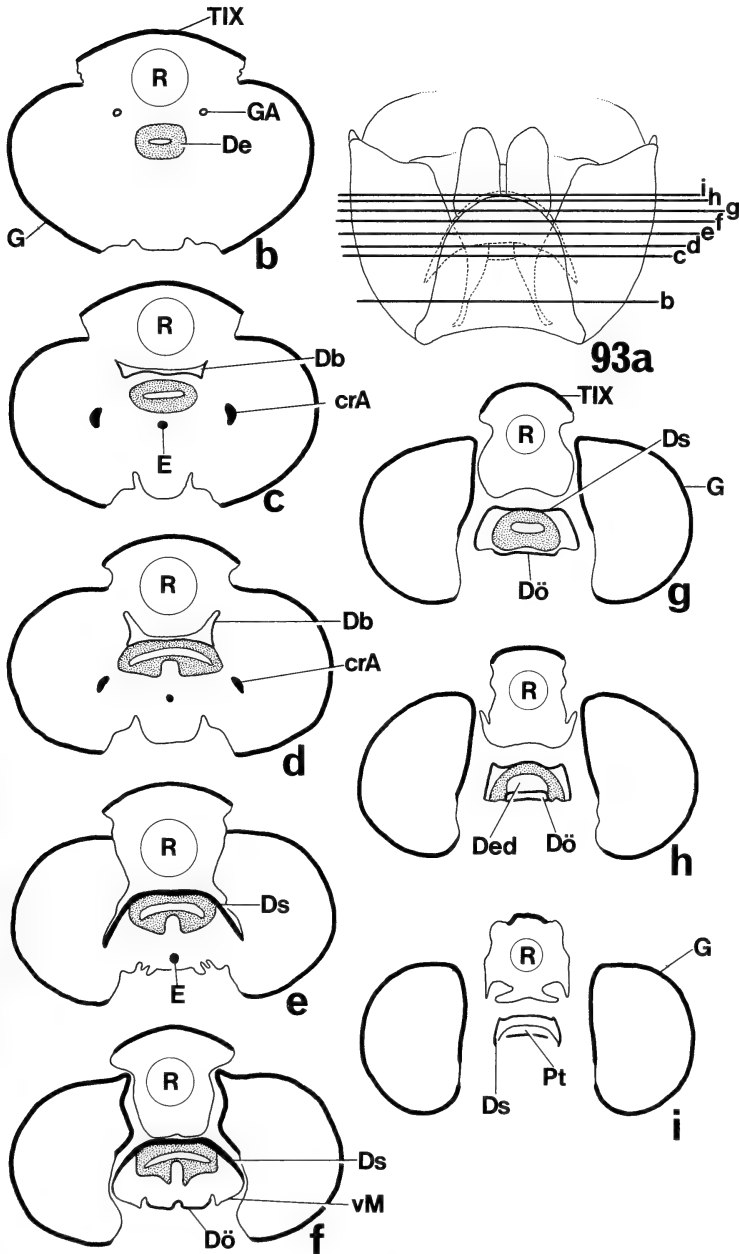
Fig.93a-i: Penis von *B. amoena*, quer (schematisch): (a) Schnittführung; (b-d) cranialer Bereich des Dorsalsklerits; (e,f) Übergang vom stabförmigen Ejaculator-Apodem in die Dörnchenplatte; (g-i) Übergang des Ductus ejaculatorius in das Phallotrema.

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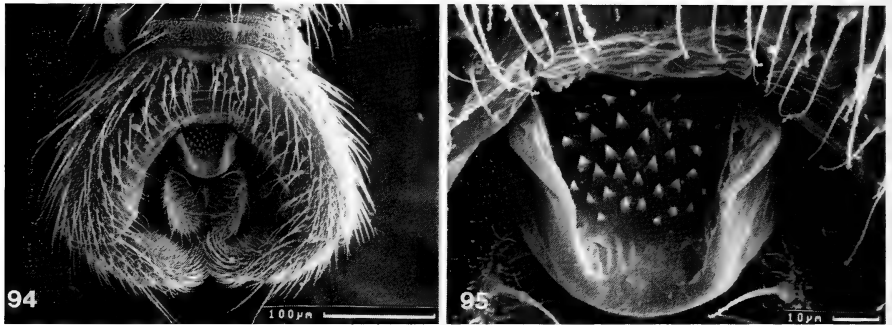
Fig.94-95: *B. amoena* ♂, REM: (94) Terminalkomplex, von ventral; (95) Dörnchenplatte, Ventralansicht.
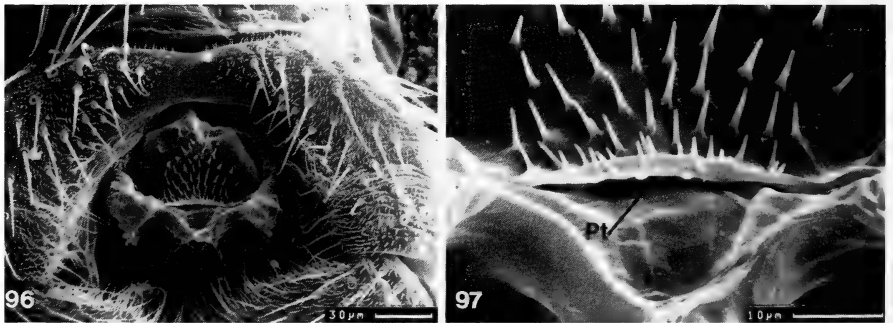
Fig.96-97: *T. trochanterata* ♂, REM: (96) Penis, von frontal; (97) Detail von (96), Phallotrema.
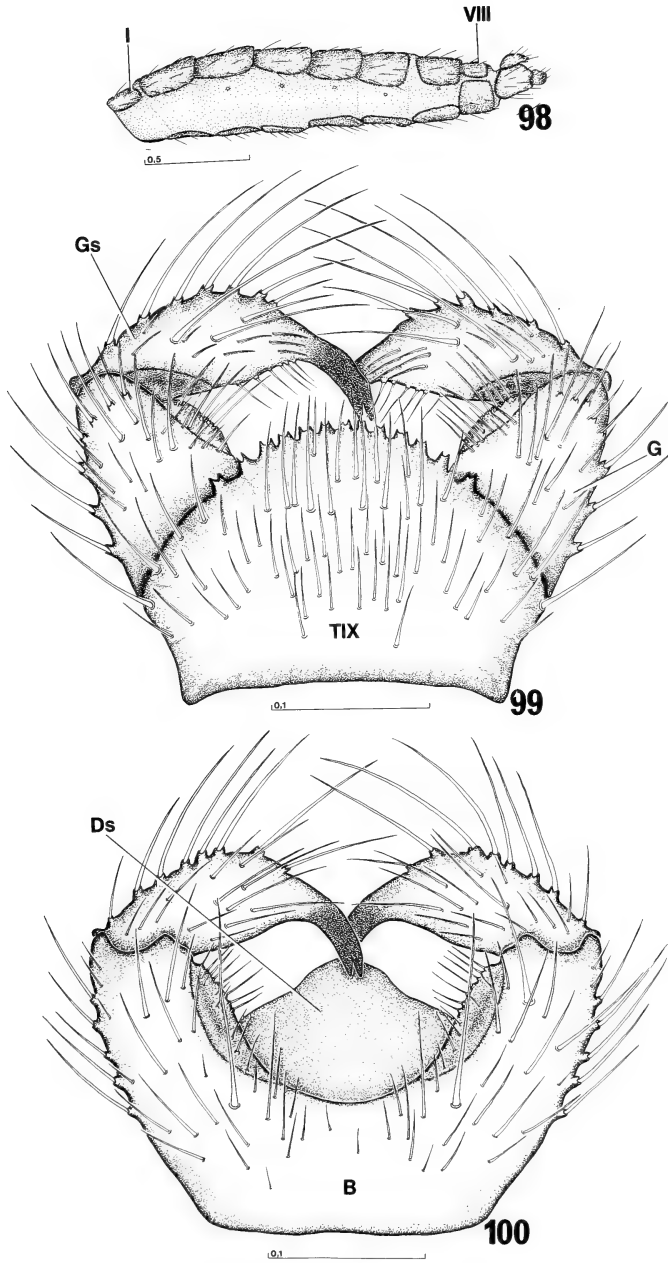
Fig.98-100: *Diadocidia ferruginosa* ♂: (98) Abdomen, von lateral; (99) Terminalia, Dorsalansicht; (100) Terminalkomplex, Ventralansicht. Maßstäbe in mm.
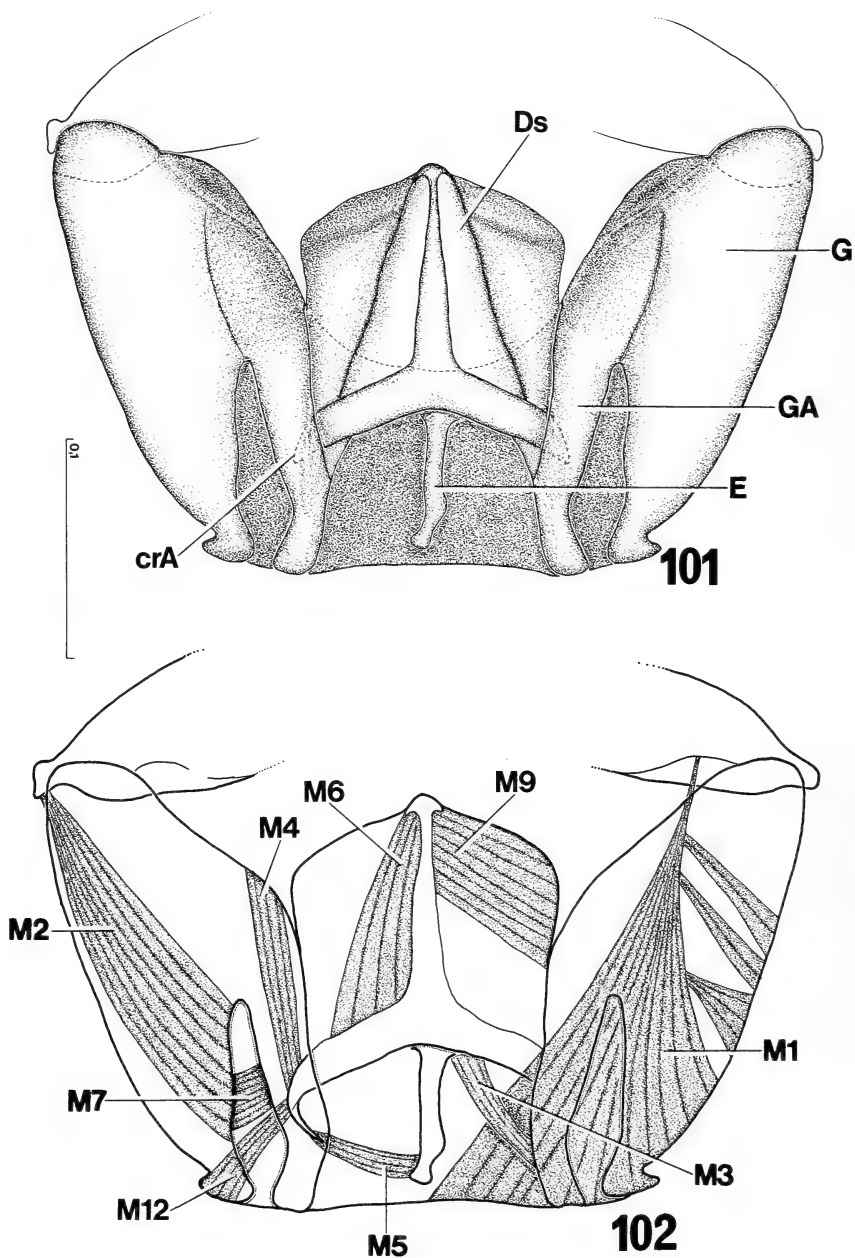
Fig.101-102: *D. ferruginosa* ♂: (101) ventrale Teile des Genitalsegments mit Penis, von dorsal; (102) dieselben Teile mit Muskulatur, von dorsal. Maßstab in mm.
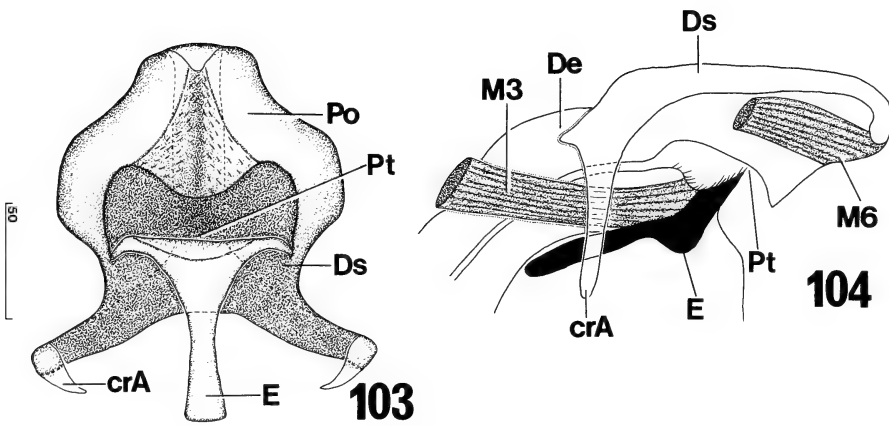
Fig.103-104: Penis von *D. ferruginosa*: (103) von ventral; (104) medio-sagittal, mit Muskulatur. Maßstab in µm.

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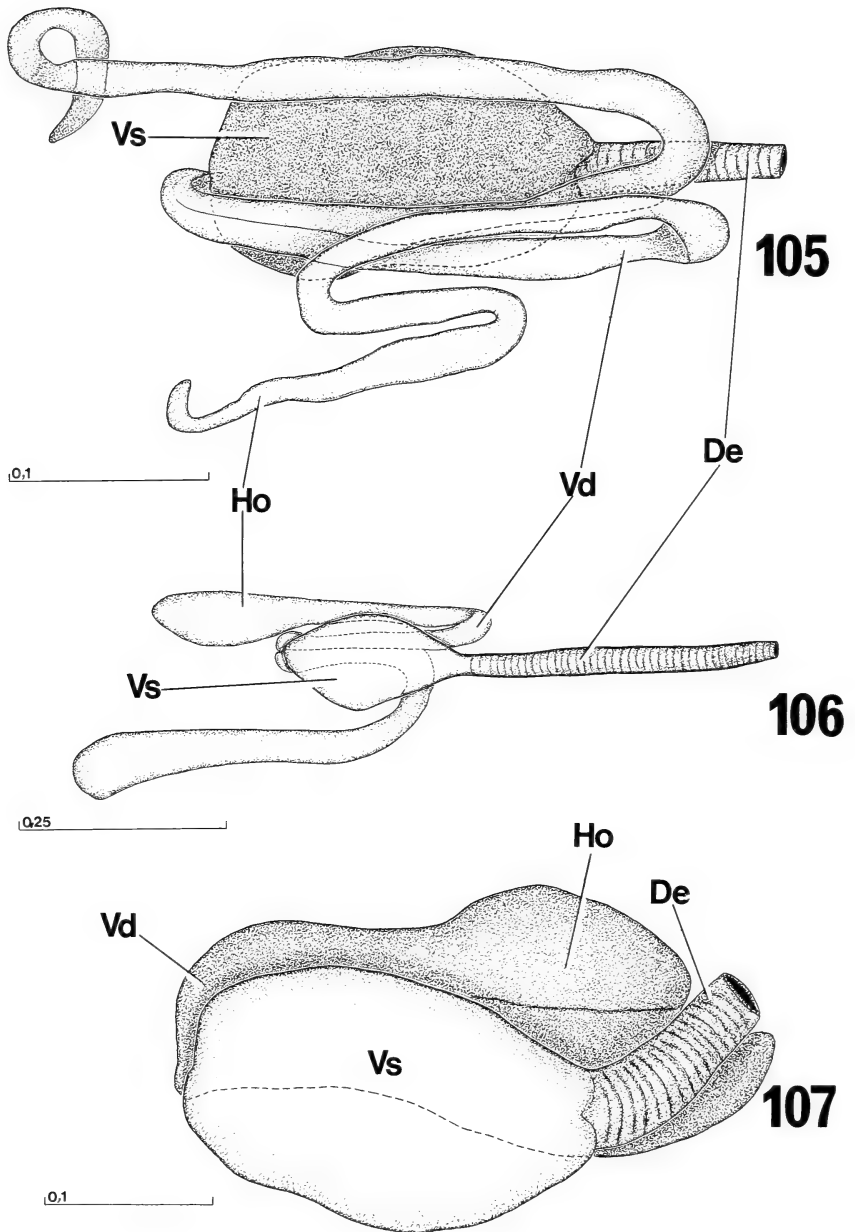
Fig.105-107: Innere Geschlechtsorgane der ♂ von (105) *Campylomyza flavipes* (Cecidomyiidae), (106) *Bradysia amoena* (Sciaridae) und (107) *Diadocidia ferruginosa* (Diadocidiidae). Maßstäbe in mm.
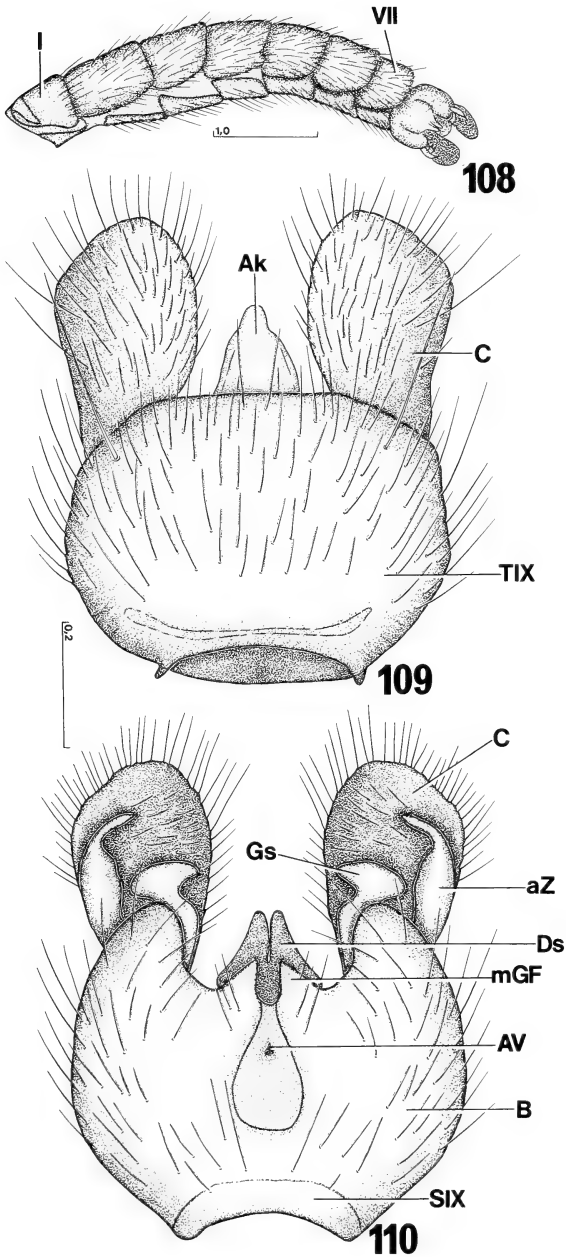
Fig.108-110: *Australosymmerus nebulosus* ♂: (108) Abdomen, von lateral; (109) Terminalkomplex, von dorsal; (110) Terminalkomplex, von ventral. Maßstäbe in mm.
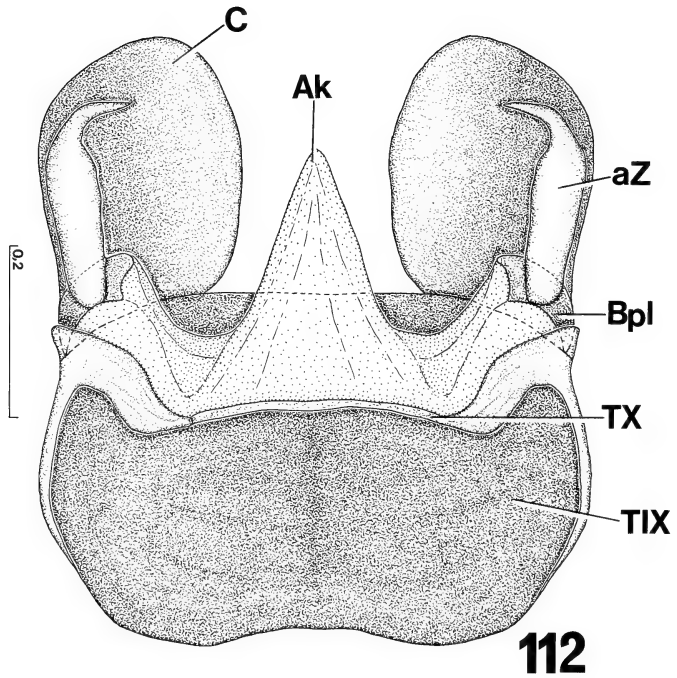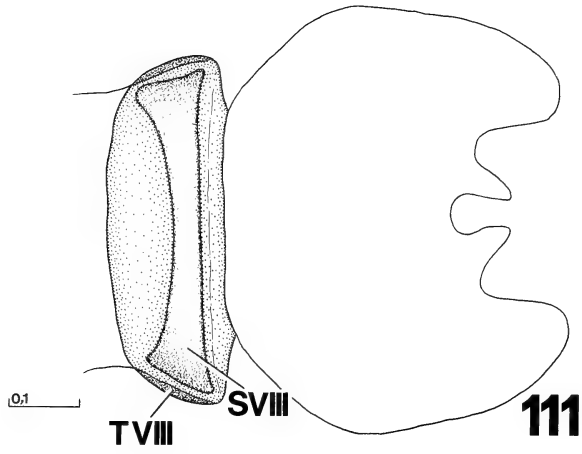
Fig.111-112: *A. nebulosus* ♂: (111) Segment VIII; (112) Analkomplex, von innen. Maßstäbe in mm.
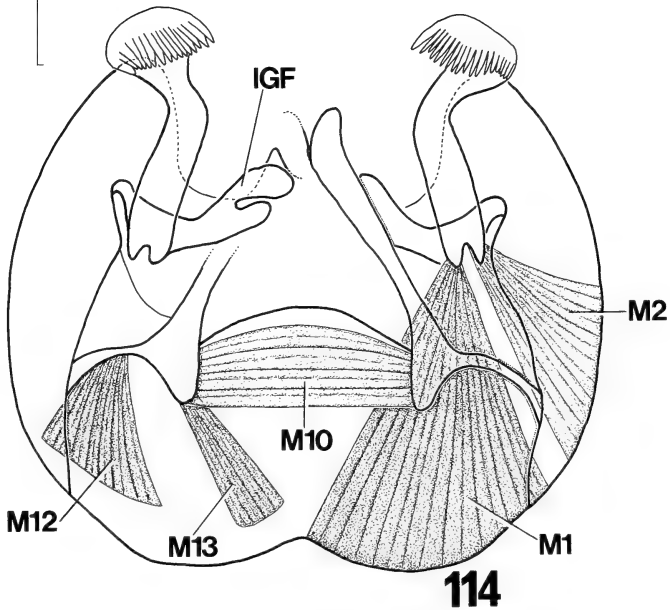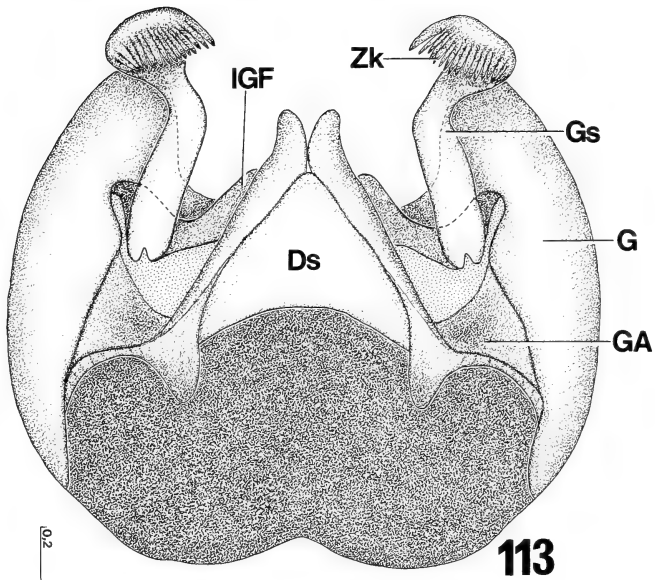
Fig.113-114: *A. nebulosus* ♂: (113) ventrale Teile des Genitalsegments mit Penis, Dorsalansicht; (114) dieselben Teile mit Muskulatur, von dorsal. Maßstab in mm.

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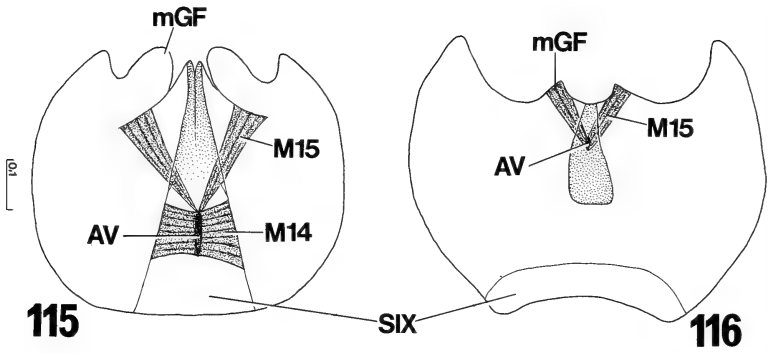
Fig.115-116: Genitalsegment-Boden mit Muskulatur von (115) *Australosymmerus fuscinervis* und (116) *A. nebulosus*. Maßstab in mm.
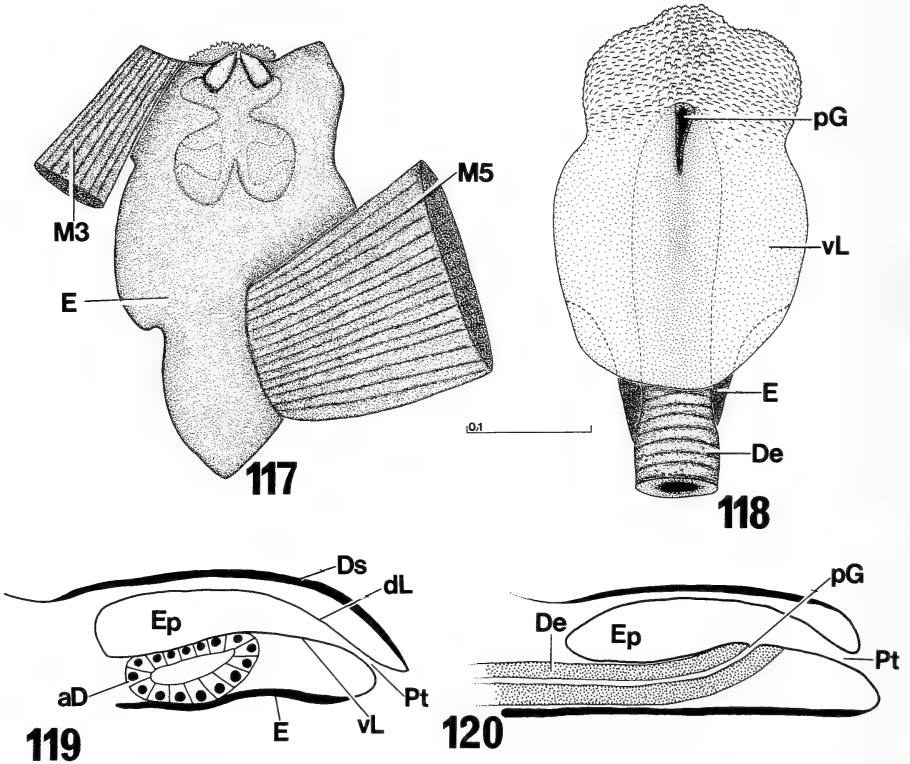
Fig.117-120: Penis von *A. nebulosus*: (117) Ejaculator-Apodem mit Muskulatur, von ventral; (118) Ventralfläche des Endophallus mit Einmündung des Ductus ejaculatorius, von innen; (119) Lage der akzessorischen Drüse ventral vom Endophallus (schematisch); (120) Penis, medio-sagittal (schematisch) (vgl. Fig.118). Maßstab in mm.
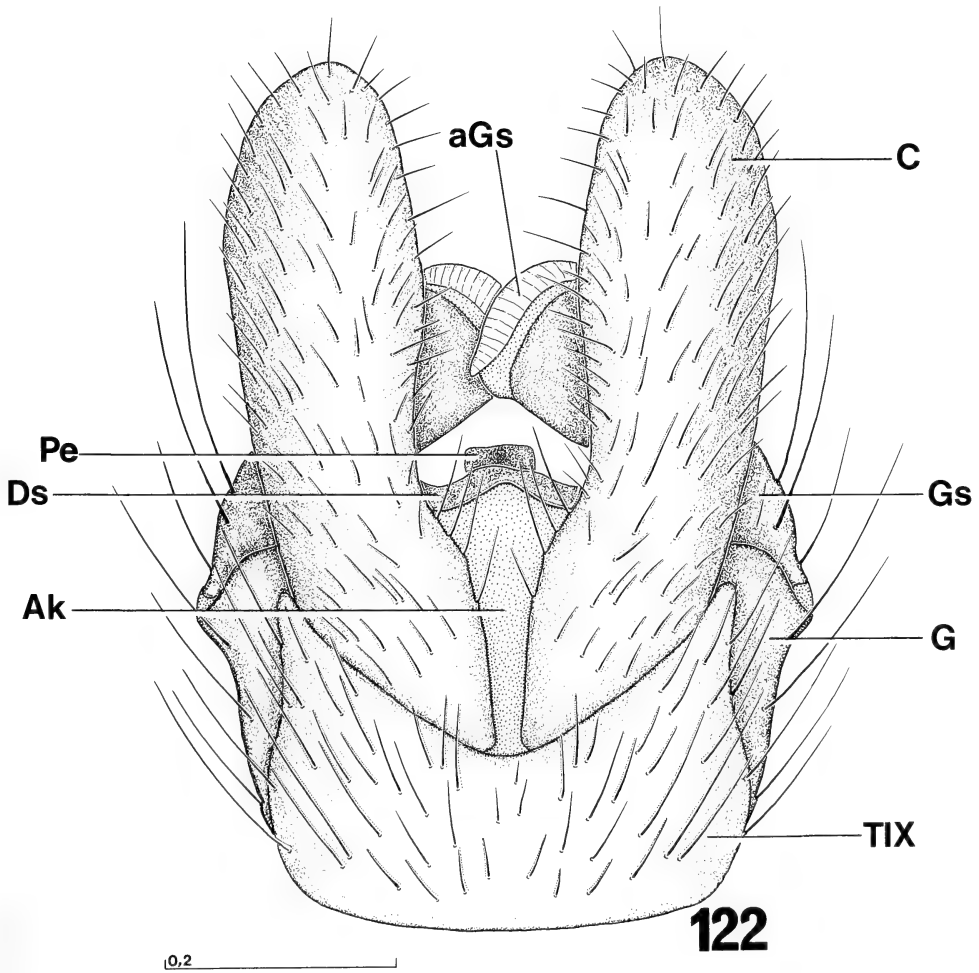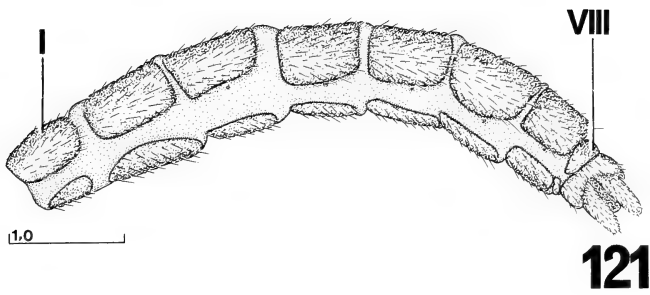
Fig.121-122: *Symmerus annulatus* ♂: (121) Abdomen, von lateral; (122) Terminalia, von dorsal. Maßstäbe in mm.

C

aGs

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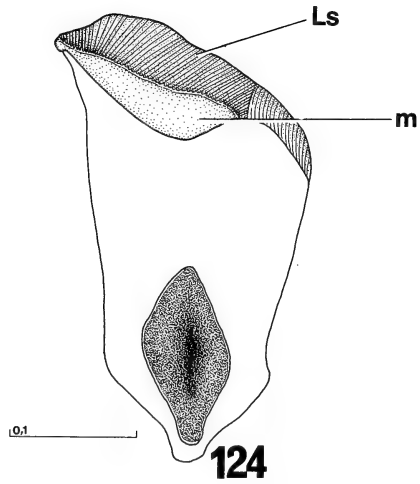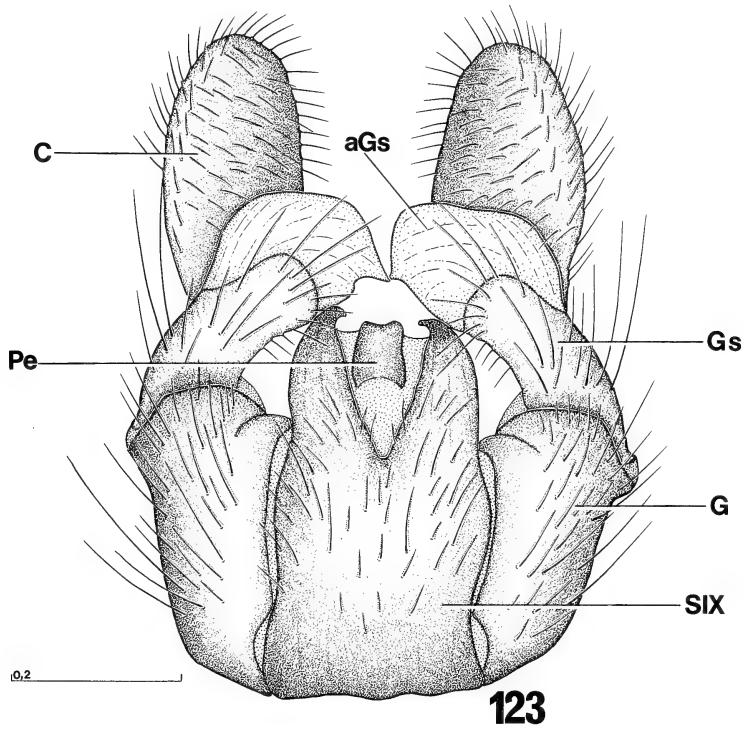
Fig.123-124: *S. annulatus* ♂: (123) Terminalkomplex, von ventral; (124) Medialfläche des Gonostylus. Maßstäbe in mm.
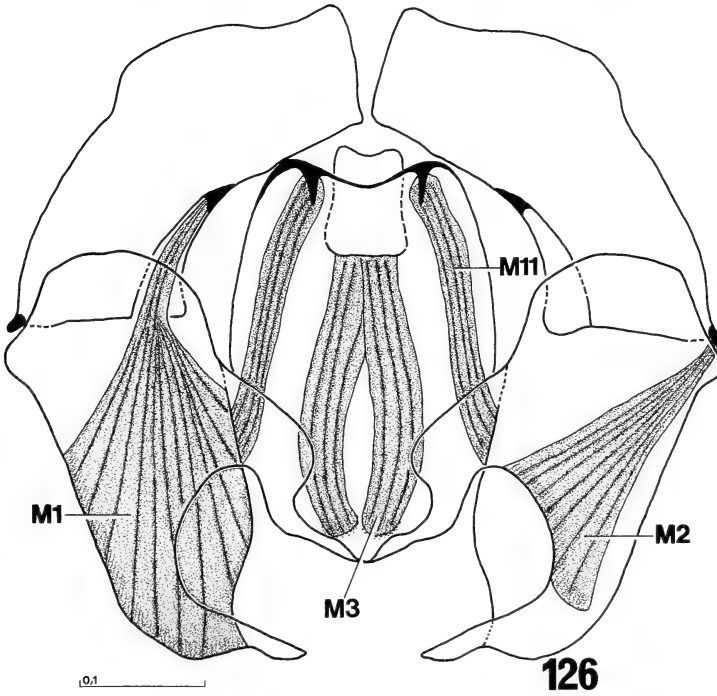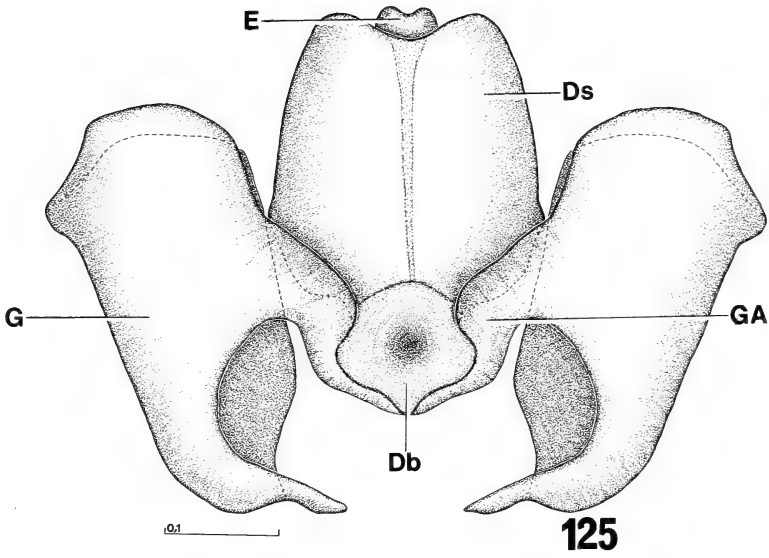
Fig.125-126: *S. annulatus* ♂: (125) Gonocoxite mit dem zwischen ihnen eingehängten Penis, Dorsalansicht; (126) Muskulatur, von dorsal. Maßstäbe in mm.
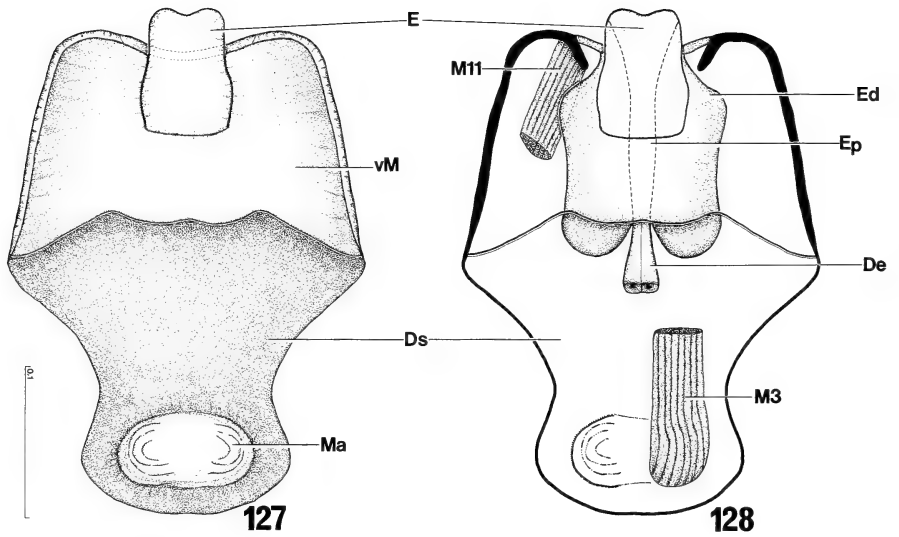
Fig.127-128: Penis von *S. annulatus*: (127) Dorsalsklerit und Ejaculator-Apodem, von ventral; (128) Muskulatur und Ductus ejaculatorius, von ventral. Maßstab in mm.
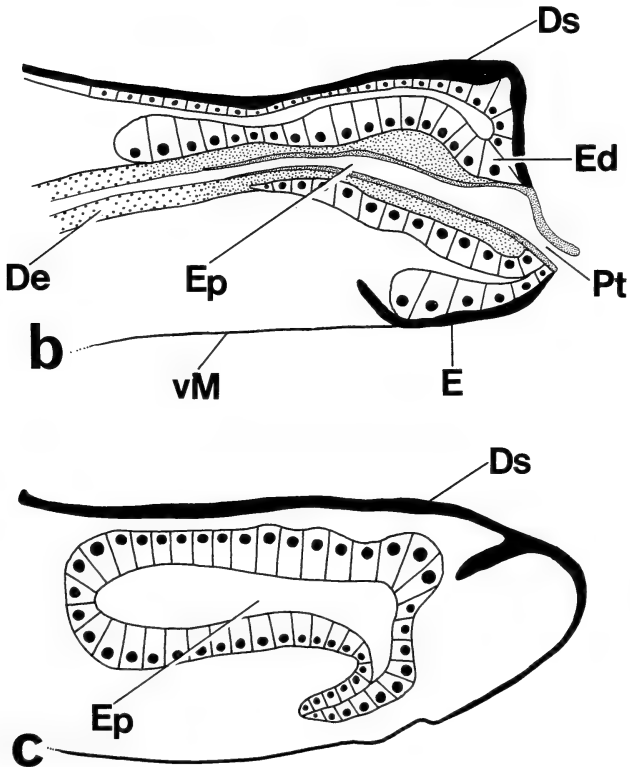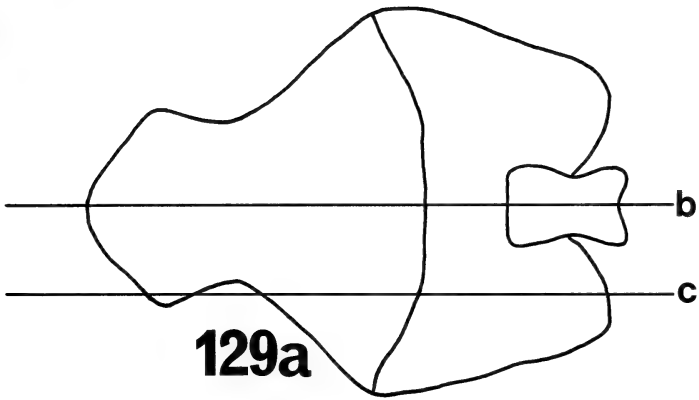
Fig.129a-c: Penis von *S. annulatus*, sagittal (schematisch): (a) Schnittführung; (b) medio-sagittal, mit Einmündung des Ductus ejaculatorius in den Endophallus; (c) lateral, im Bereich des Endophallus.

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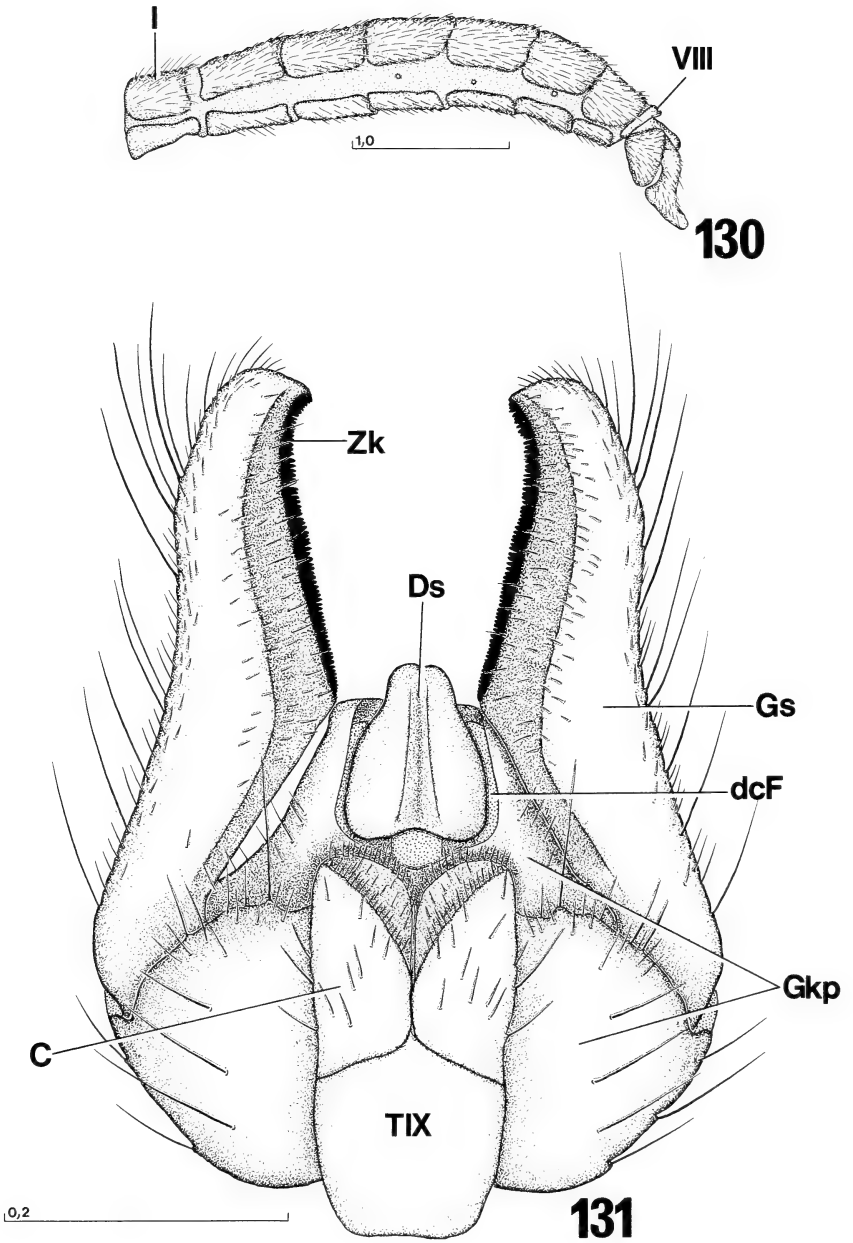
Fig.130-131: *Ditomyia fasciata* ♂: (130) Abdomen, Lateralansicht; (131) Terminalia, von dorsal. Maßstäbe in mm.
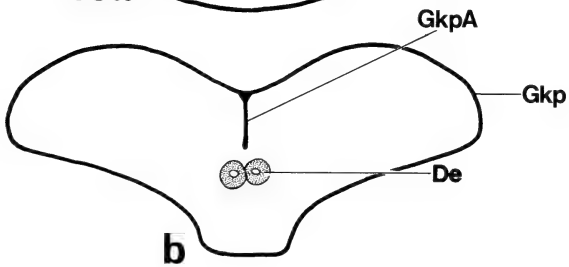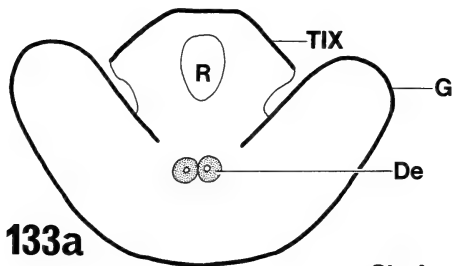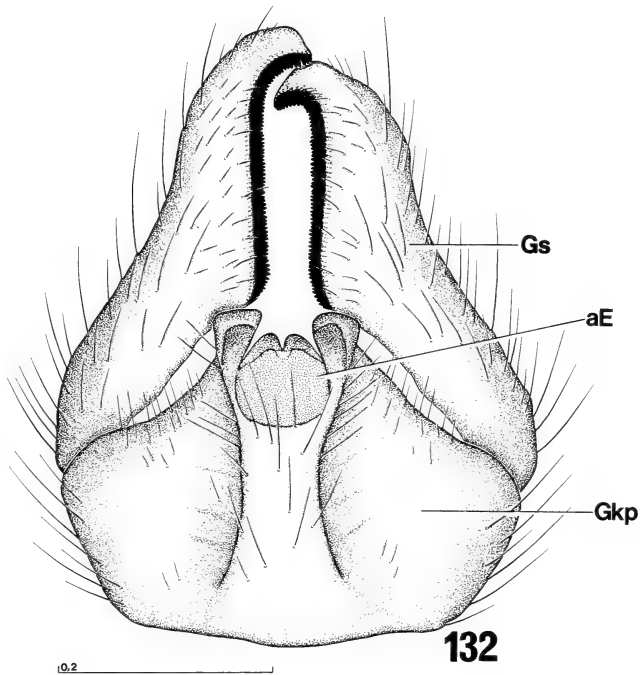
Fig.132-133: *D. fasciata* ♂: (132) Terminalia, von ventral; (133a) Genitalkapsel quer (schematisch) im Bereich des Analkomplexes; (133b) Genitalkapsel quer weiter caudal - die Genitalkapsel bildet hier ein Apodem (GkpA) aus. Maßstab in mm.
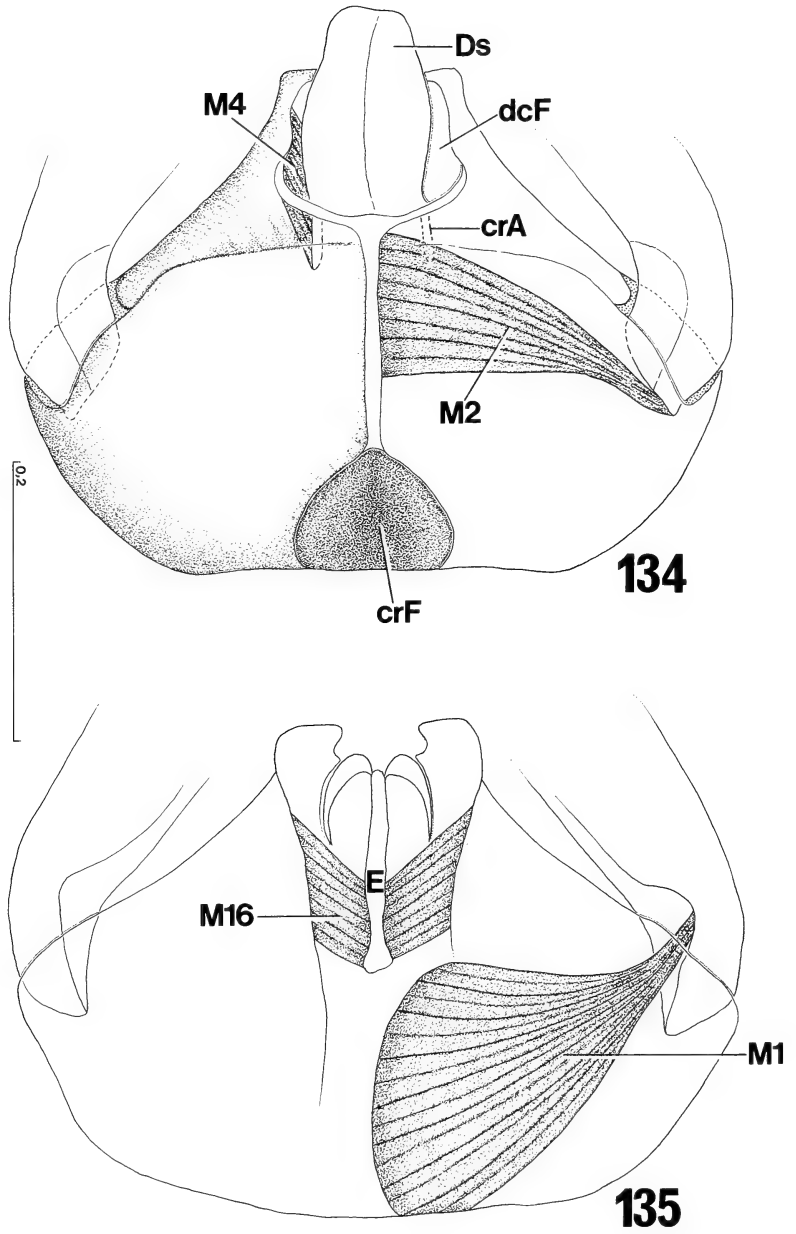
Fig.134-135: *D. fasciata* ♂: (134) Genitalkapsel mit Muskulatur, von dorsal; (135) Genitalkapsel mit Muskulatur, von ventral. Maßstab in mm.
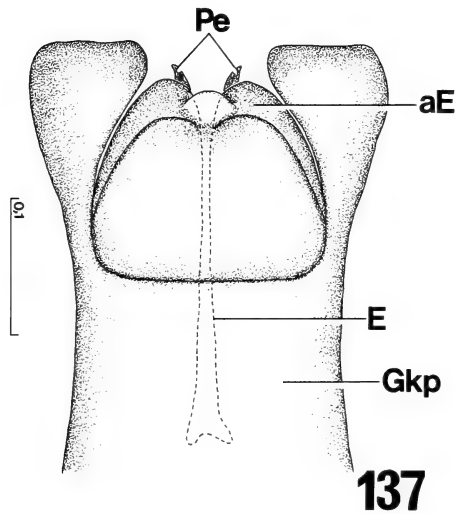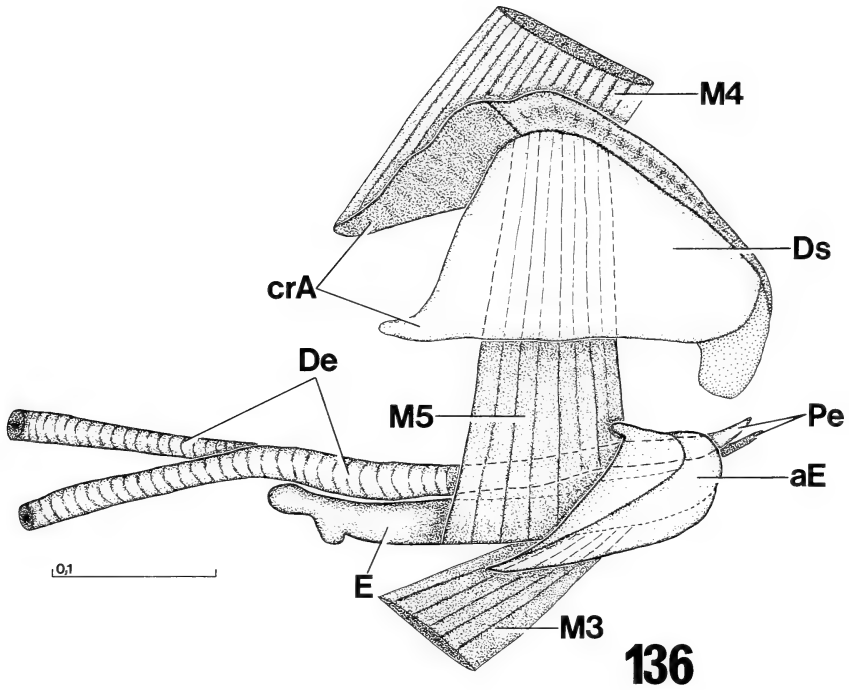
Fig.136-137: Penis von *D. fasciata*: (136) mit Dorsalsklerit und Muskulatur, Lateralansicht; (137) Zusammenhang von Genitalkapsel und Ejaculator-Apodem, von ventral. Maßstäbe in mm.

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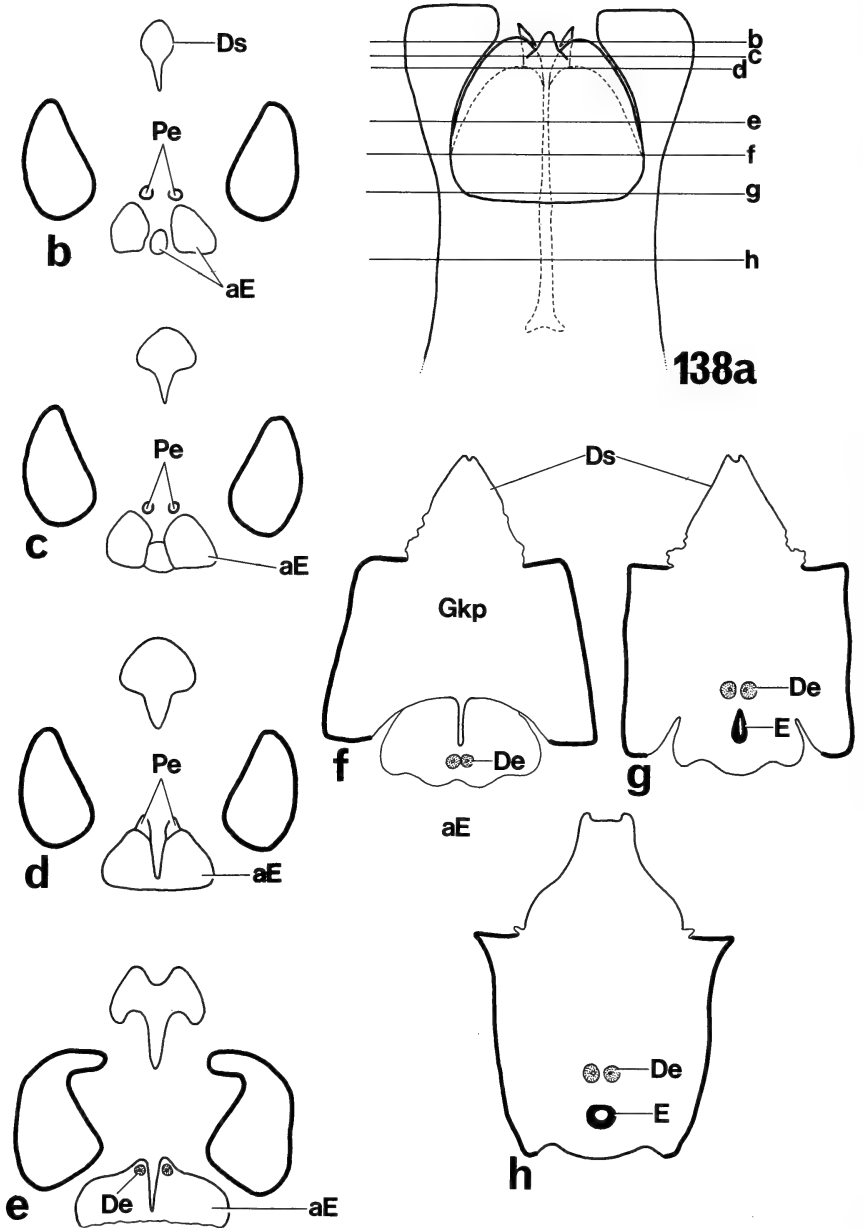
Fig.138a-h: Genitalkapsel von *D. fasciata*, quer (schematisch): (a) Schnittführung; (b-d) Übergang der Penes in das Ejaculator-Apodem; (e,f) Zusammenhang von Ejaculator-Apodem und Genital-kapsel; (g,h) Genitalkapsel im stabförmigen Bereich des Ejaculator-Apodems.
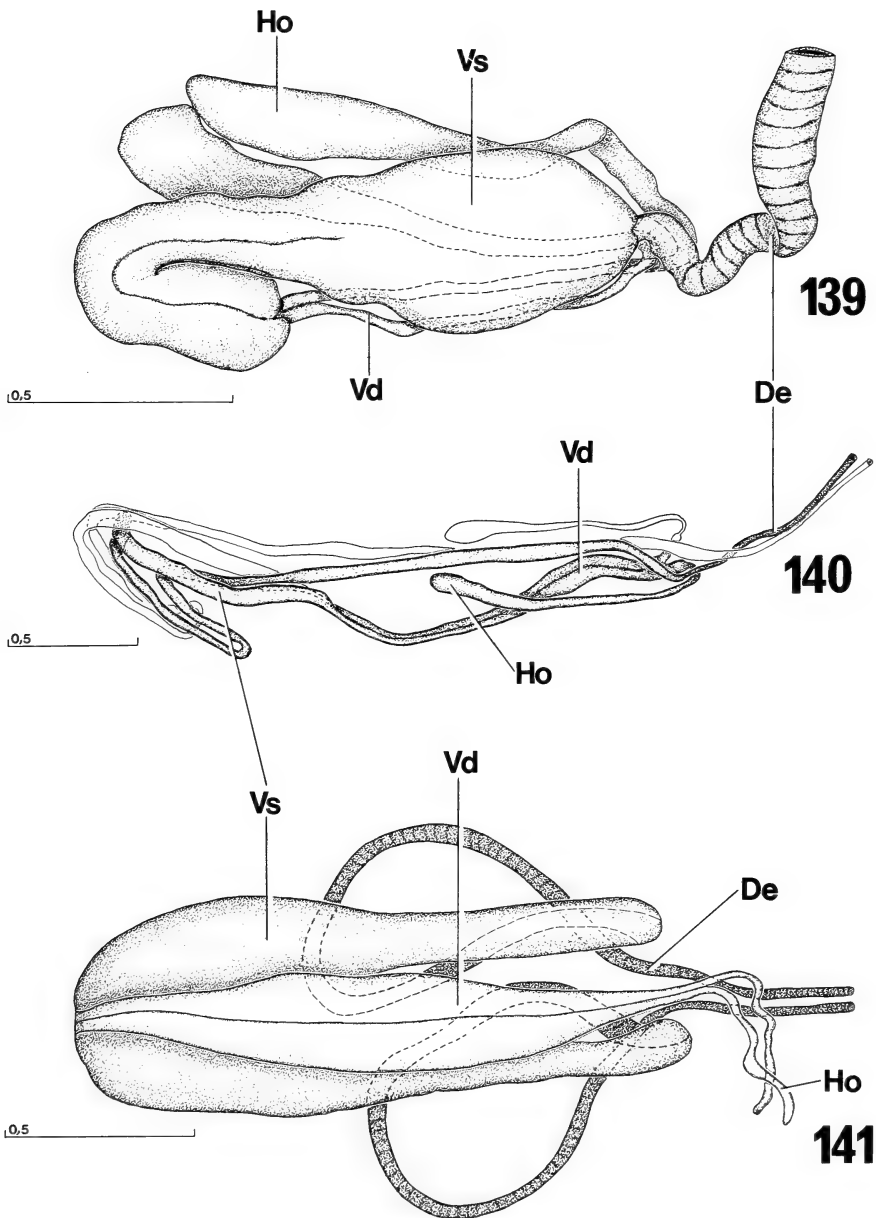
Fig.139-141: Männliche innere Geschlechtsorgane von (139) *Australosymmerus nebulosus*, (140) *Symmerus annulatus* und (141) *Ditomyia fasciata*. Maßstäbe in mm.
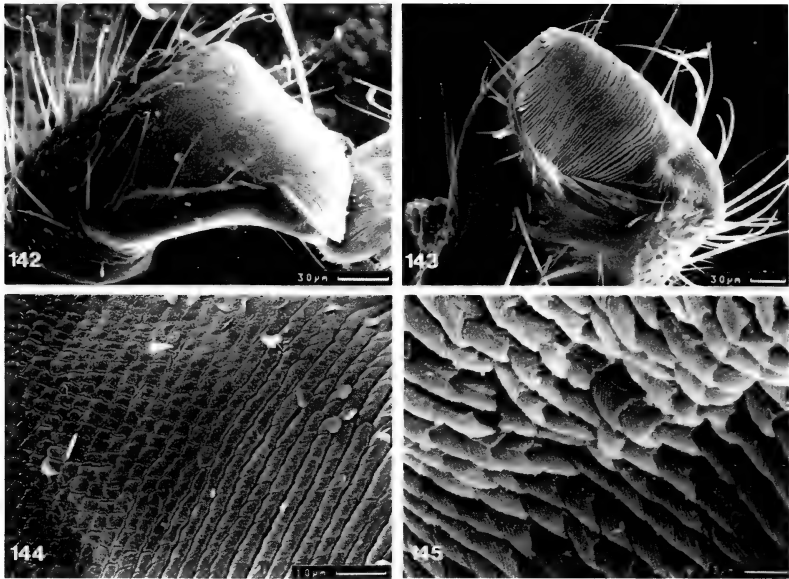
Fig.142-145: Gonostylus von *S. annulatus*, REM: (142) von dorsal; (143) von medial; (144) Lamellen auf der Dorsalseite; (145) Lamellen auf der Medialseite.
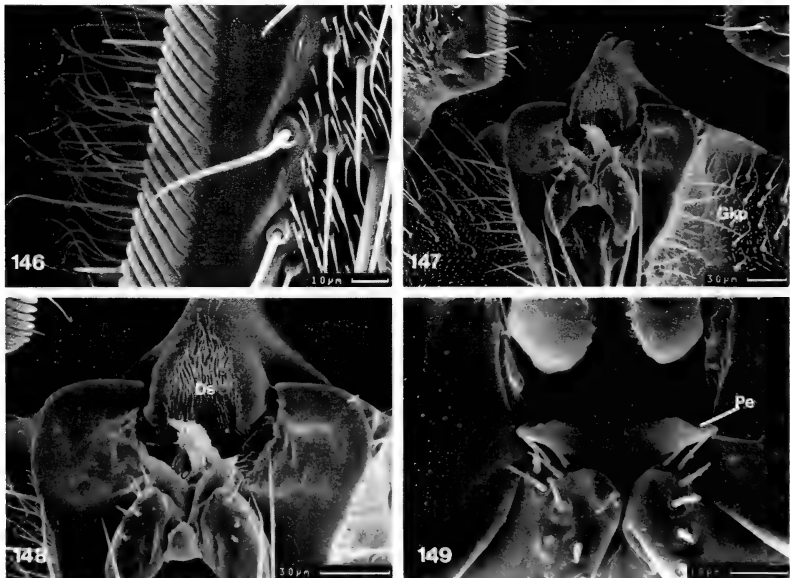
Fig.146-149: *D. fasciata*, REM: (146) Zähnchenkamm des Gonostylus; (147) Genitalkapsel, von frontal; (148) Detail von (147), Dorsalsklerit mit dichter Behaarung; (149) Penes, von frontal.
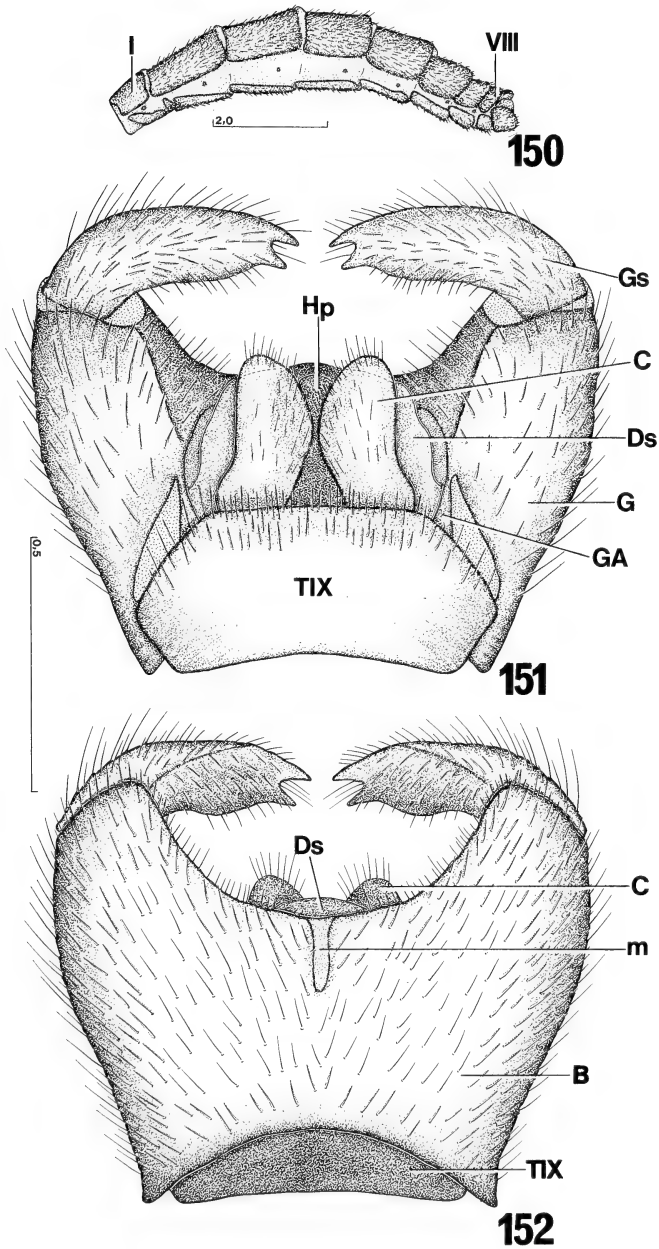
Fig.150-152: *Platyura marginata* ♂: (150) Abdomen, von lateral; (151) Terminalkomplex, von dorsal; (152) Terminalkomplex, von ventral. Maßstäbe in mm.
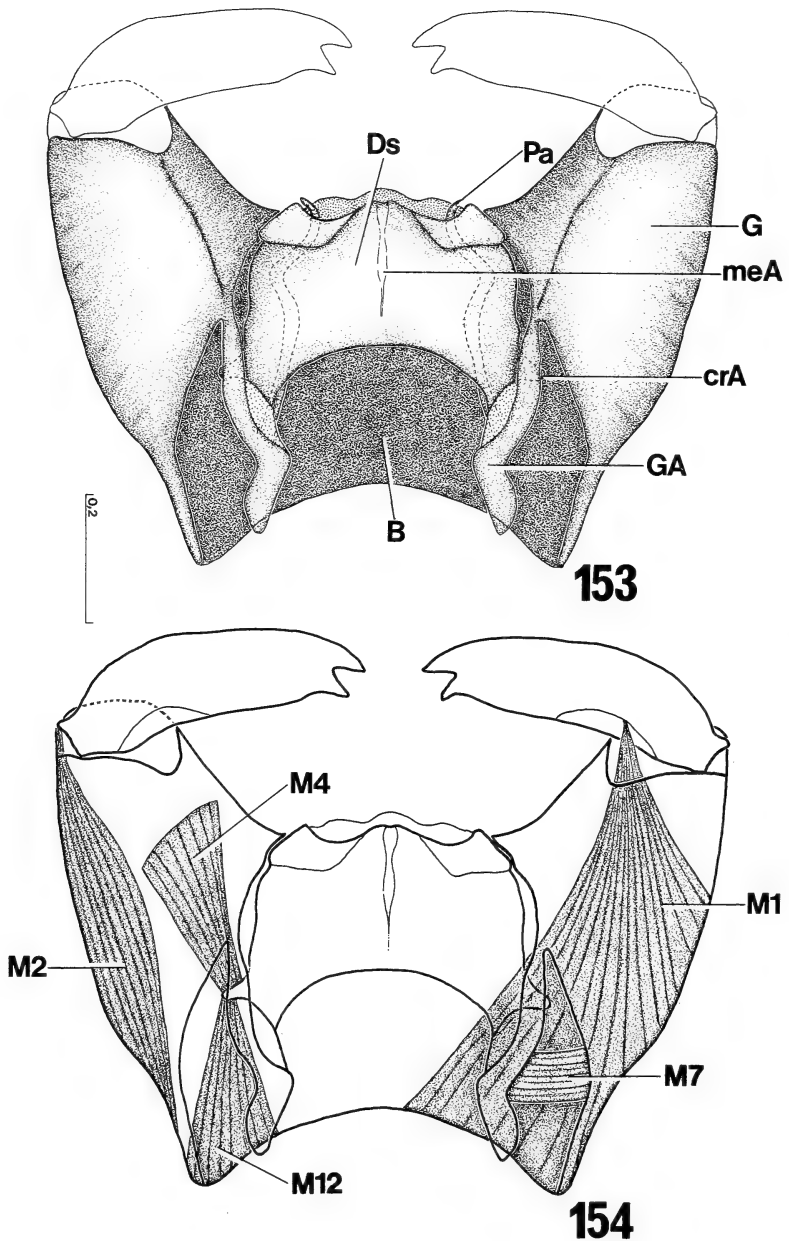
Fig.153-154: *P. marginata* ♂: (153) ventrale Teile des Genitalsegments mit Penis, von dorsal; (154) dieselben Teile mit Muskulatur, Dorsalansicht. Maßstab in mm.
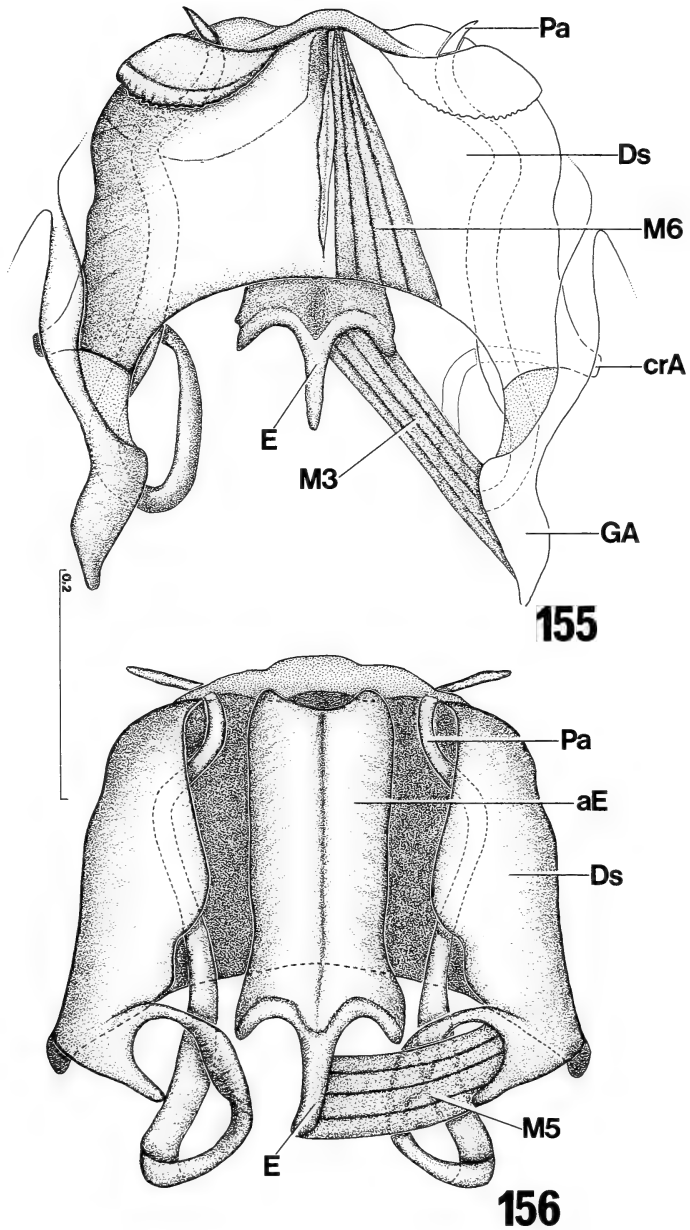
Fig.155-156: Penis von *P. marginata*: (155) Dorsalsklerit und Ejaculator-Apodem mit Muskulatur, von dorsal; (156) Dorsalsklerit und Ejaculator-Apodem mit Muskulatur, von ventral. Maßstab in mm.
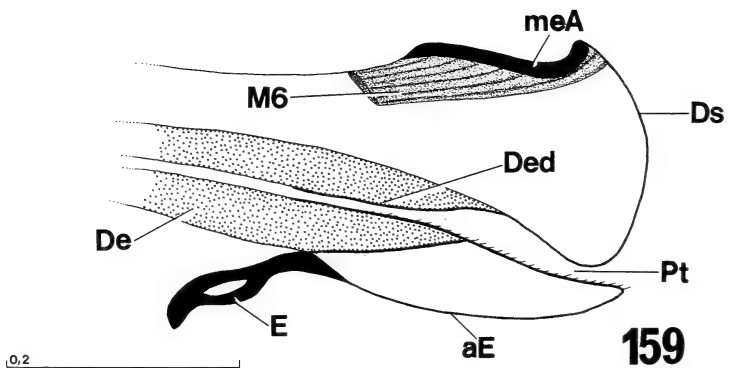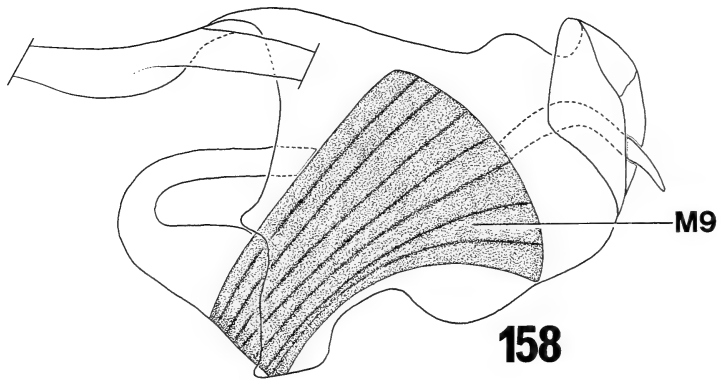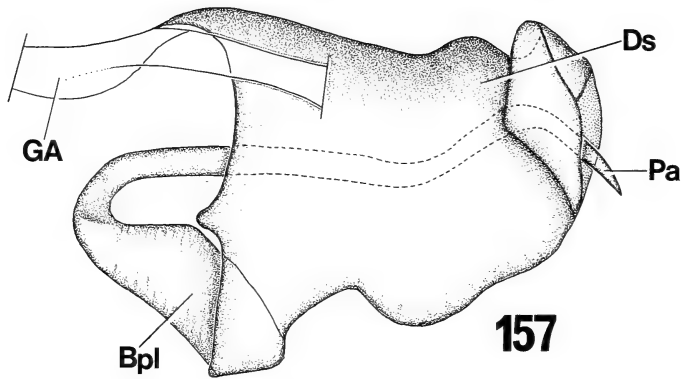
Fig.157-159: Penis von *P. marginata*: (157) sklerotisierte Elemente, von lateral; (158) Lateralansicht, mit Parameren-Muskel (M9); (159) medio-sagittal, Übergang des Ductus ejaculatorius in den Ductus ejaculatorius distalis. Maßstab in mm.
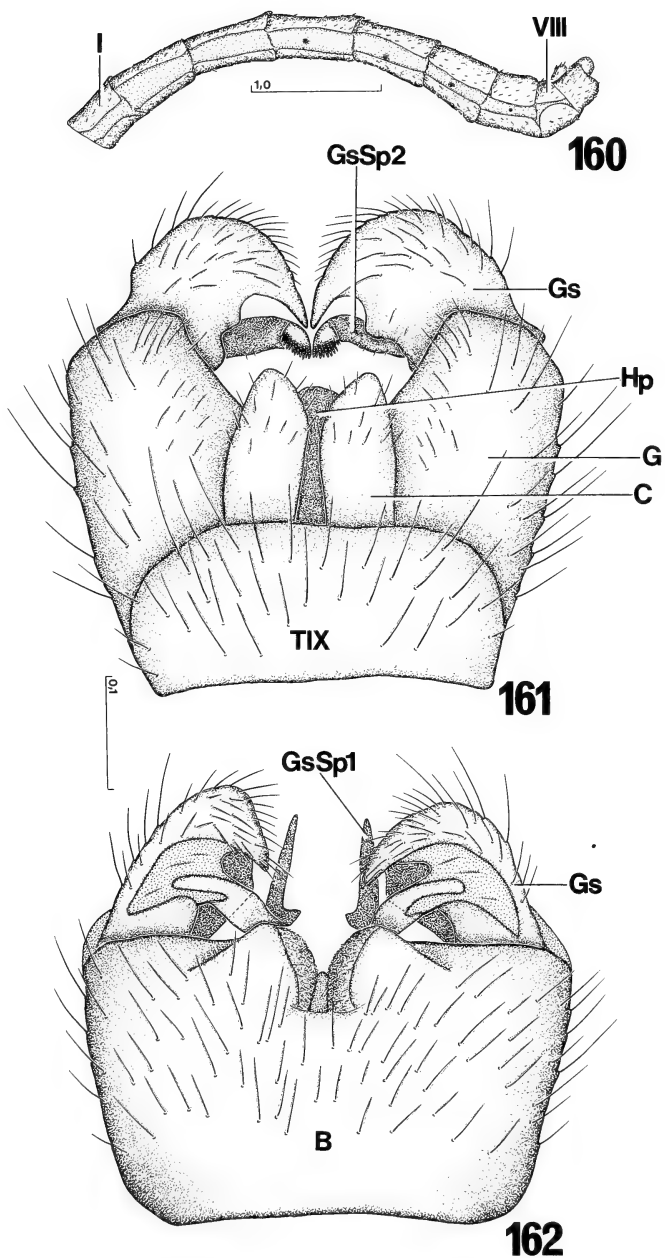
Fig.160-162: *Bolitophila tenella* ♂: (160) Abdomen, von lateral; (161) Terminalkomplex, von dorsal; (162) Terminalkomplex, von ventral. Maßstäbe in mm.
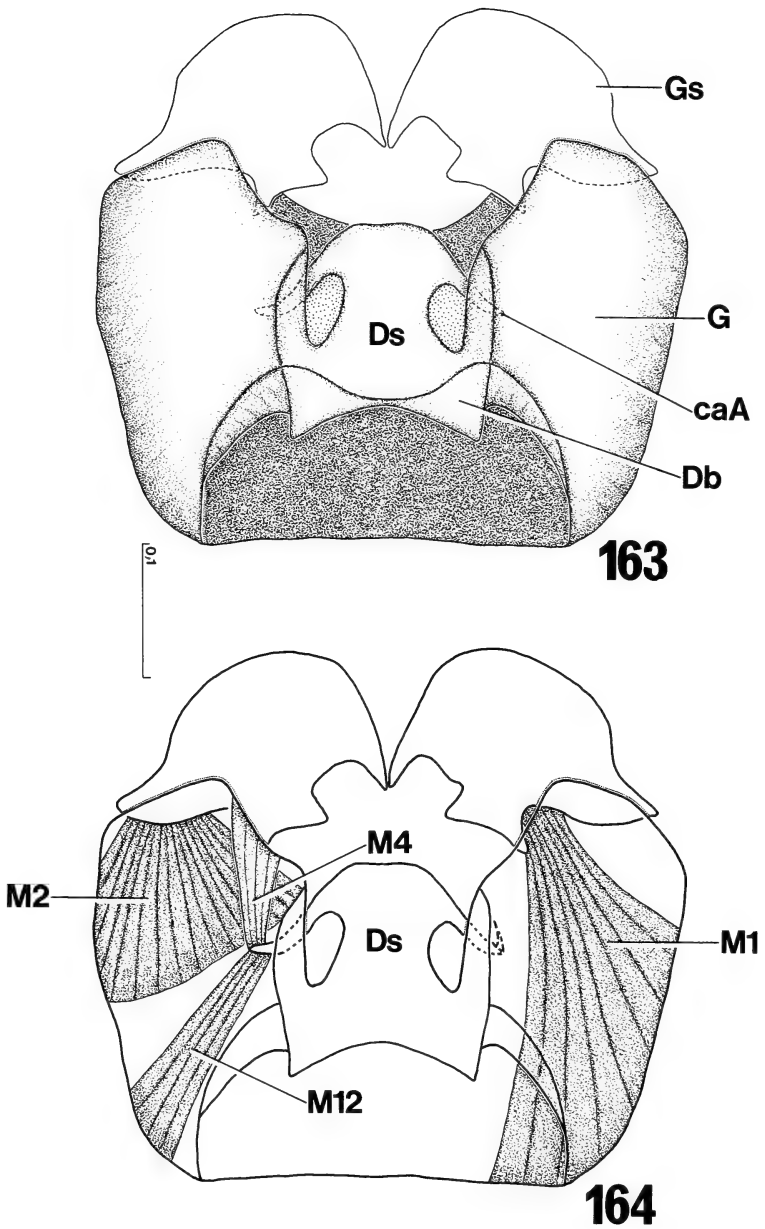
Fig.163-164: ventrale Teile des Genitalsegments mit Penis von *B. tenella*; (163) Exoskelett; (164) Muskulatur. Maßstab in mm.
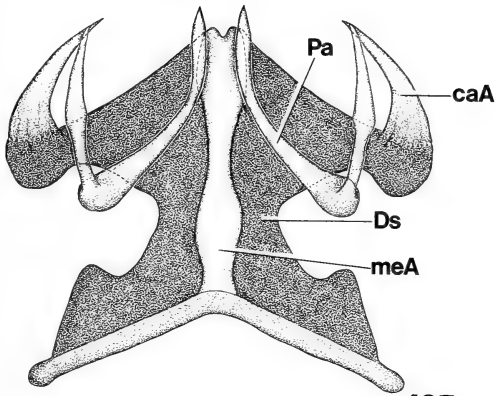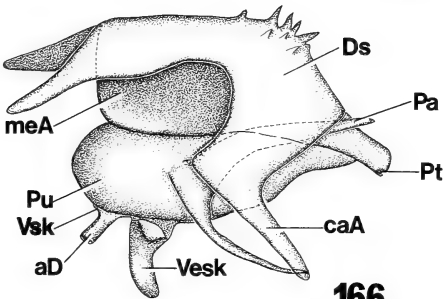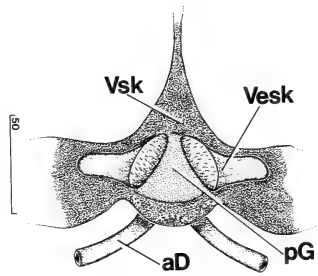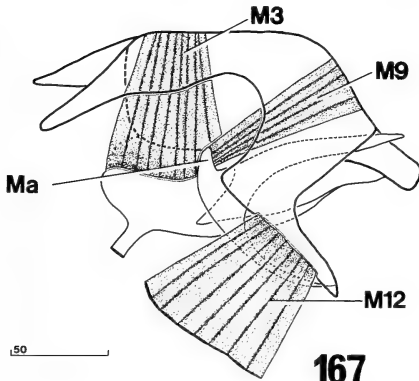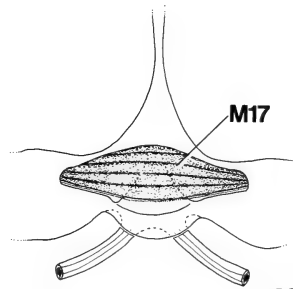
Fig.165-169: Penis von *B. tenella*; (165) Dorsalsklerit mit Parameren, von innen; (166) der gesamte Komplex, von lateral; (167) Muskulatur. (168) Pumpenkomplex (Ausschnitt), von ventral; der primäre Gonoporus (pG) öffnet sich — umgeben von dem paarigen Ventilsklerit (Vesk) — in den Pumpenvorraum des Penis. (169) unpaarer Muskel, der zwischen den beiden Ventilskleriten ausgespannt ist. Maßstab in μm.
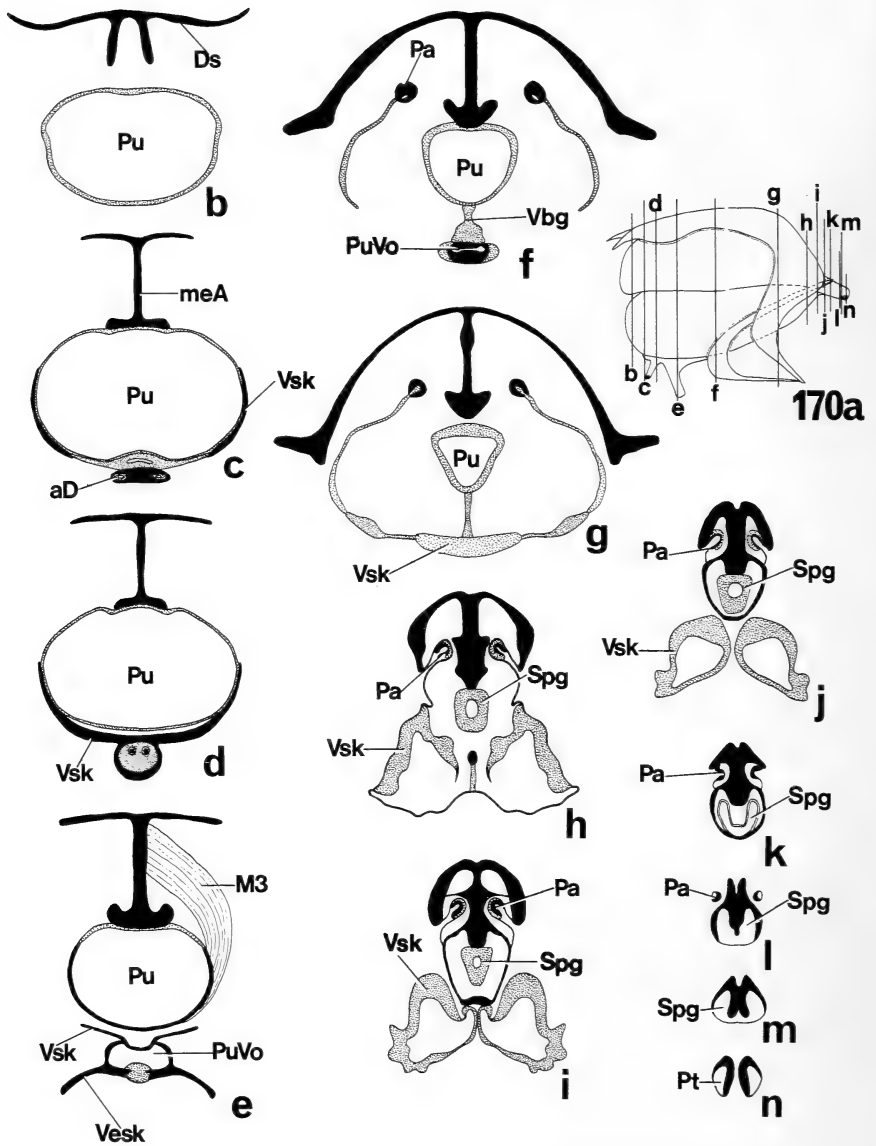
Fig.170a-n: Spermapumpe von *B. tenella*, quer (schematisch): (a) Schnittführung; (b,c,d) Verbindung des Pumpen-Apodems (meA) mit dem Pumpen-Raum (Pu), Einmündung der akzessorischen Drüse in den Pumpen-Vorraum; (e) Pumpen-Muskulatur (M3), die bei Kontraktion das Apodem in den Pumpen-Raum zieht, und Pumpen-Vorraum (PuVo) mit den Ventilskleriten (Vesk); (f-j) das Lumen des Pumpen-Raums wird zunehmend eingeengt, die Wandung dicker; zwischen Pumpen-Vorraum und Pumpen-Raum befindet sich ein Gewebestrang, in dem vermutlich ein Verbindungsgang (Vbg) verläuft; apikal wird das Ventralsklerit (Vsk) paarig und ist weniger stark sklerotisiert; (k-n) der Spermagang geht in den Endabschnitt des Penis über; der Gang wird durch einen Zapfen, der ein Ausläufer des Pumpen-Apodems ist, in zwei Hälften geteilt, so daß das Phallotrema paarig ist.
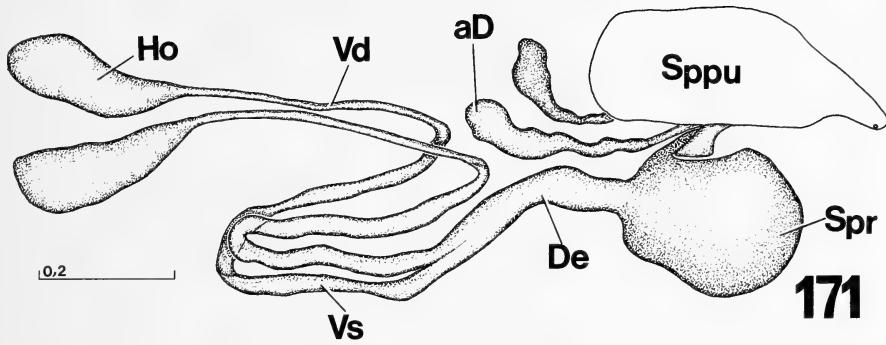
Fig.171: *B. tenella* innere Geschlechtsorgane und ihre Lagebeziehung zur Spermapumpe (Sppu): Ventral vom Pumpenkomplex befindet sich eine sackartige Erweiterung des Ductus ejaculatorius, das Spermareservoir, in dem Sperma vor der Kopulation gespeichert wird. Maßstab in mm.
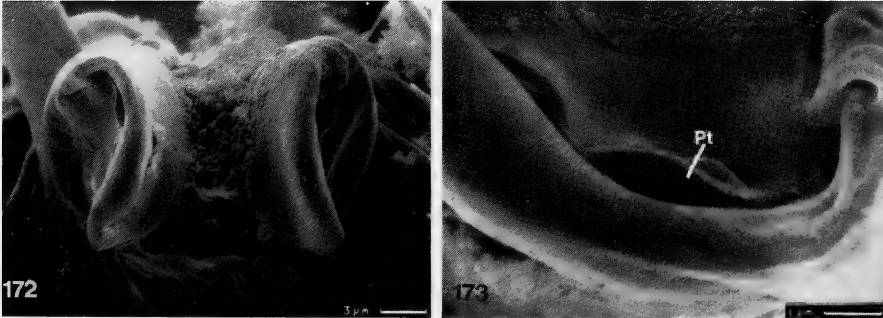
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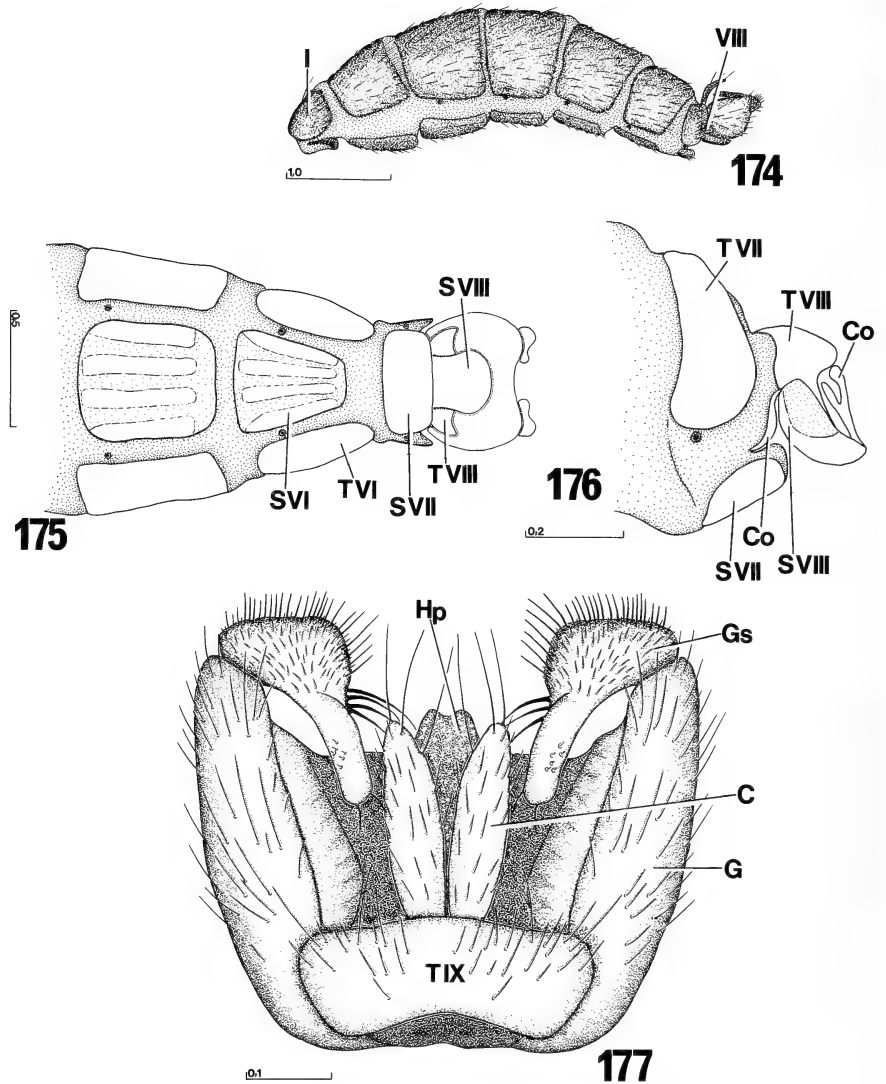
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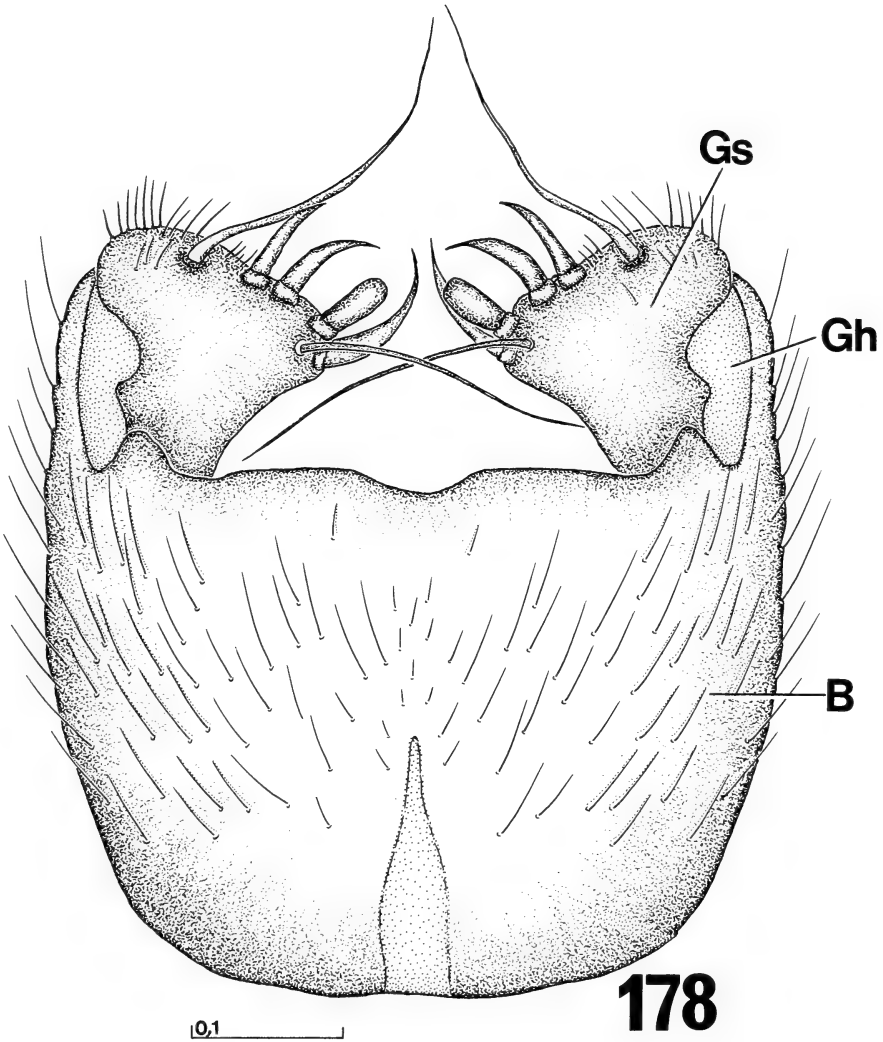
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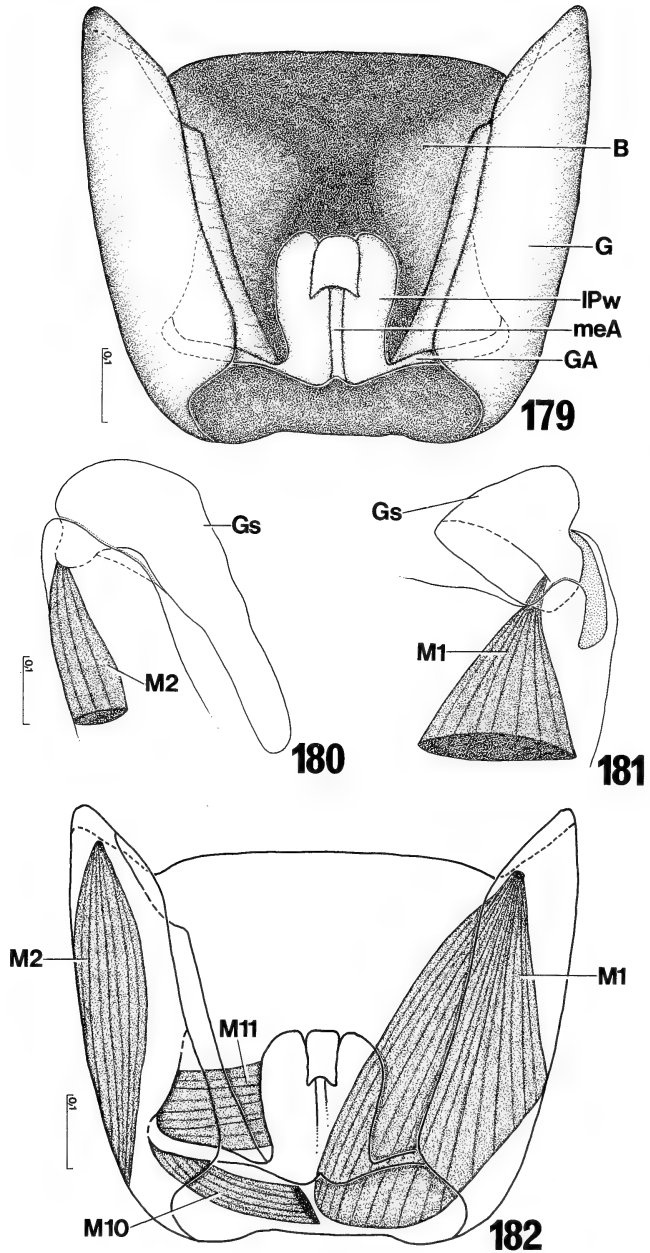
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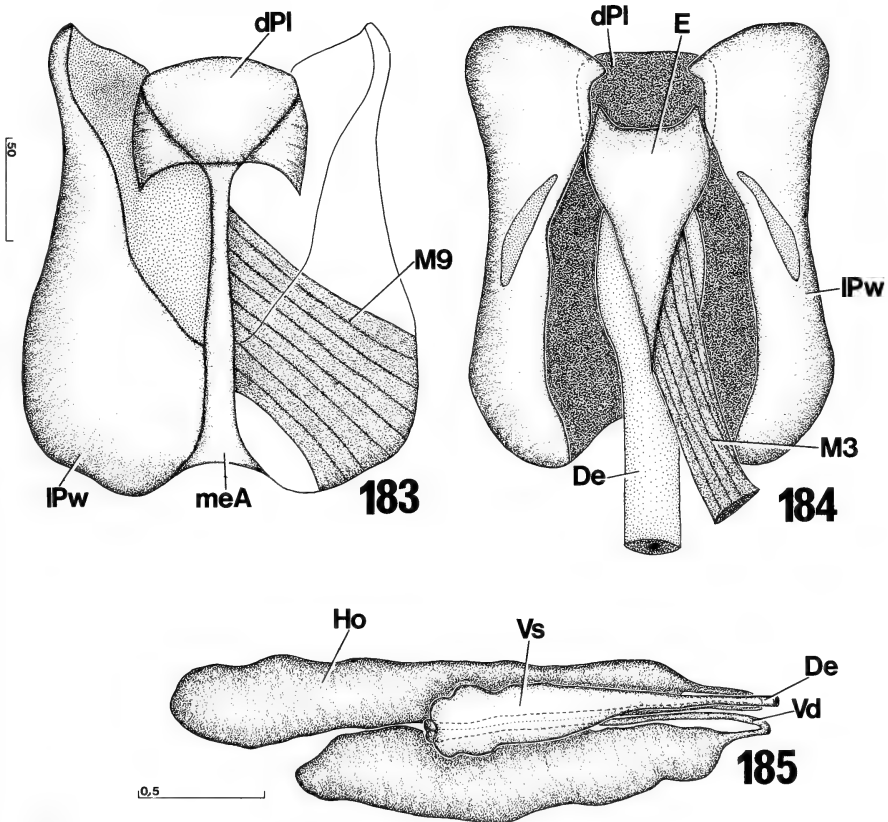
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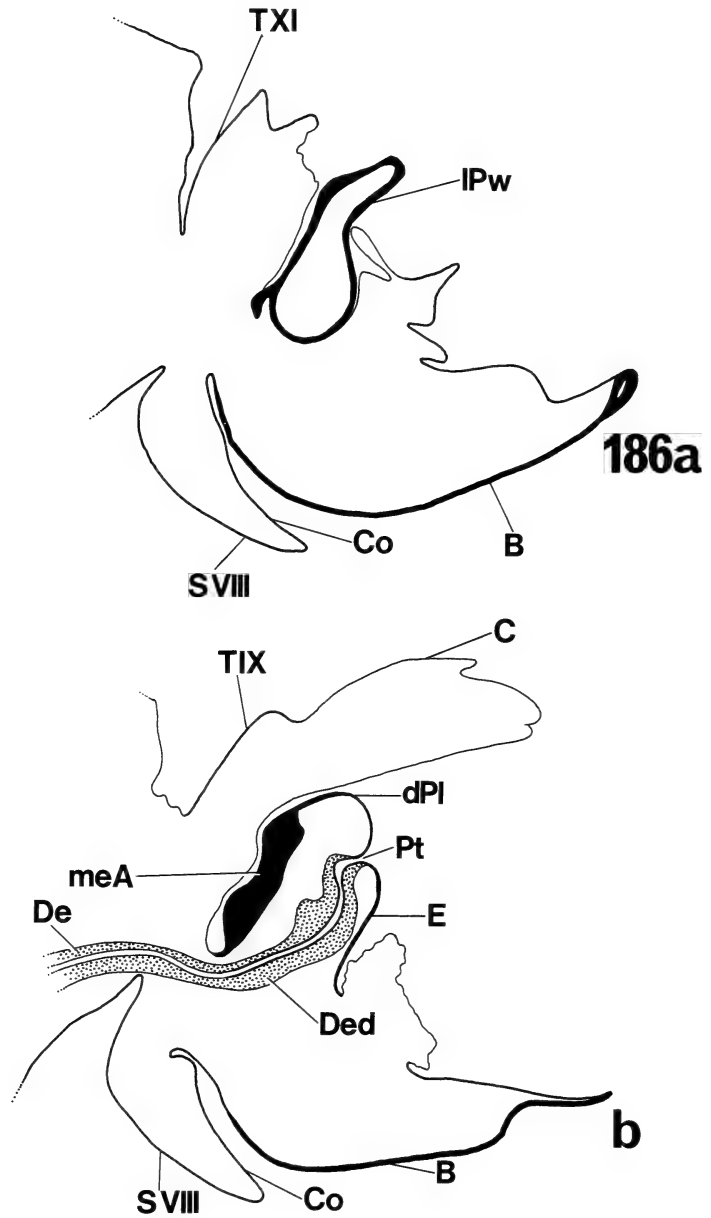
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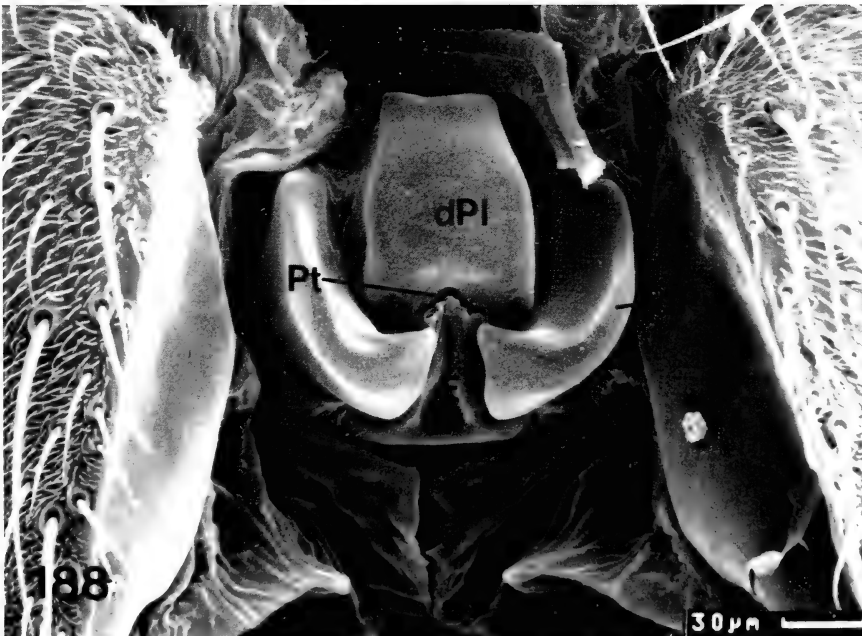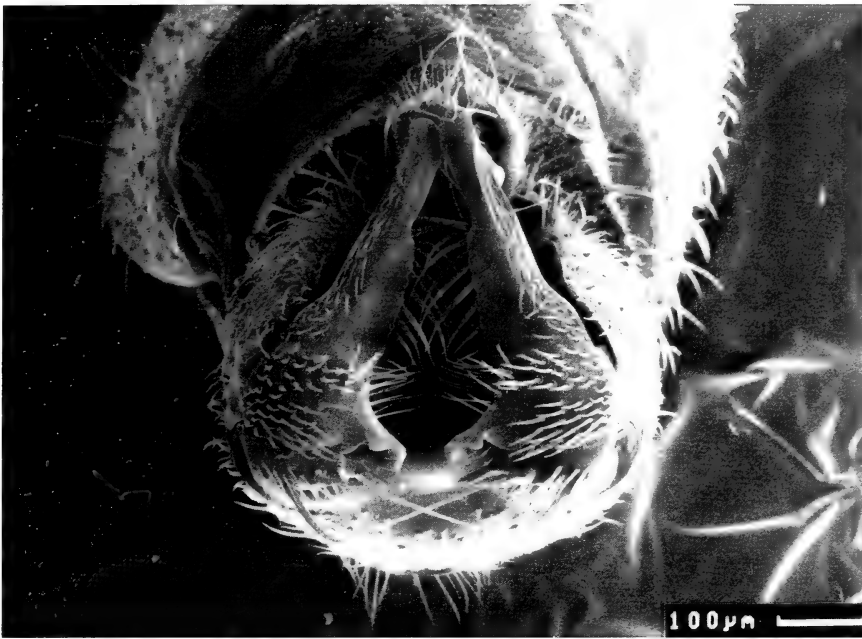
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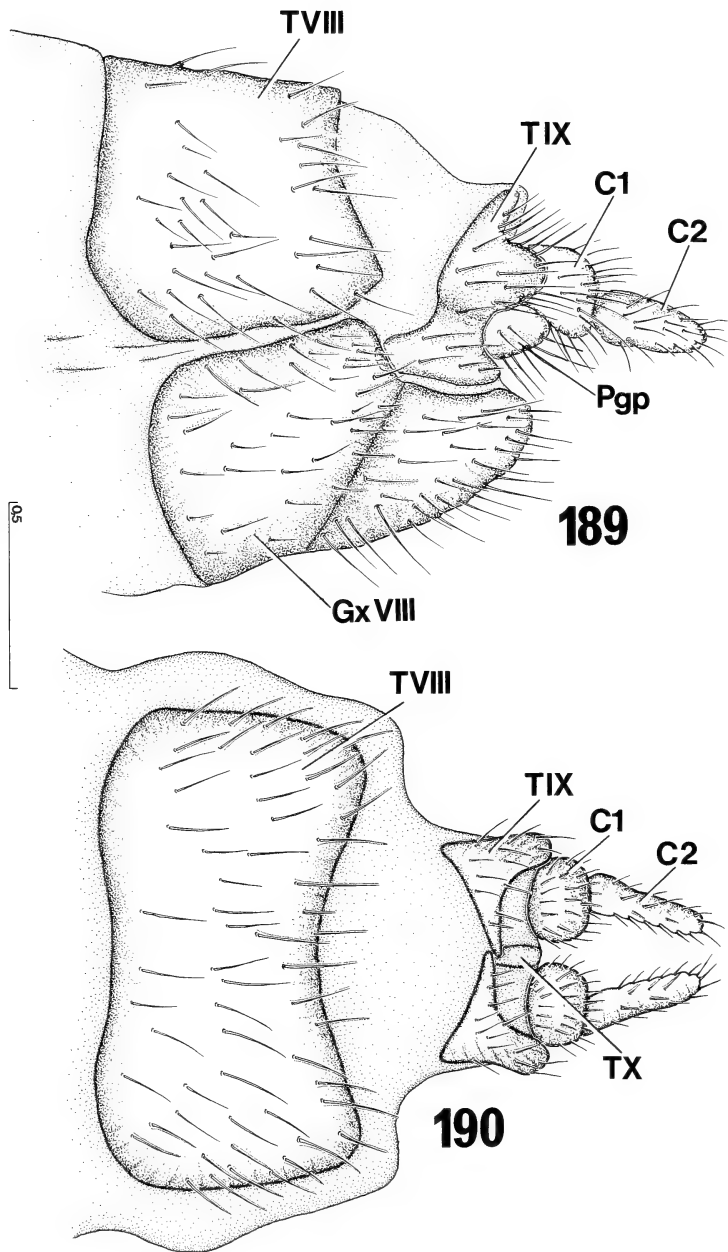
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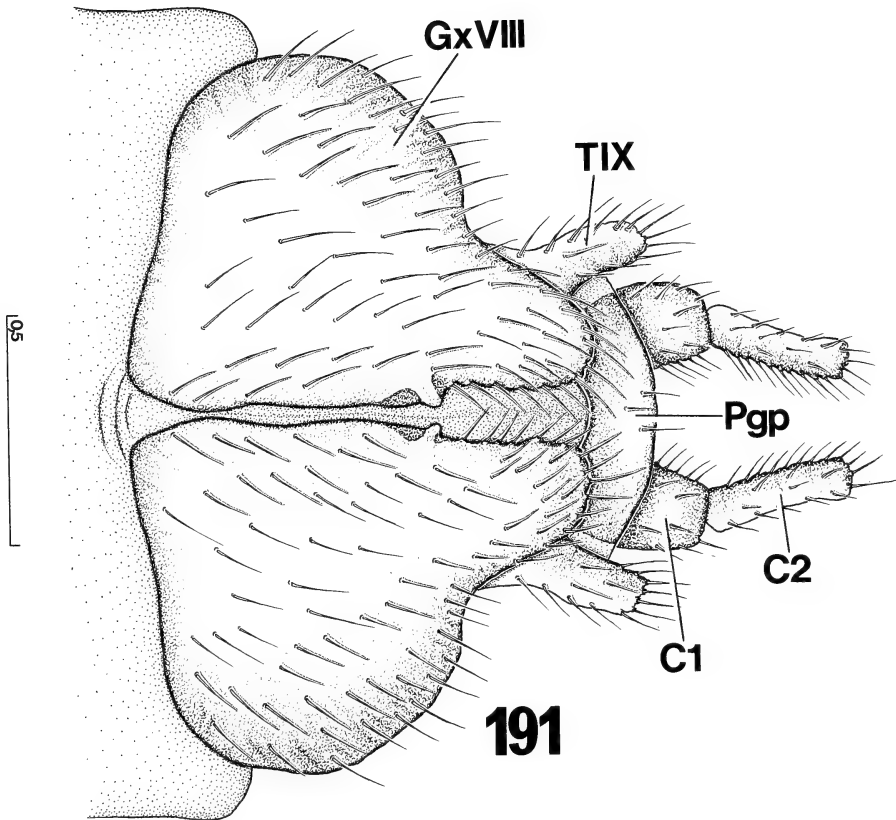
Fig.191: Legeröhre von *P. funebris*, Exoskelett, von ventral. Maßstab in mm.

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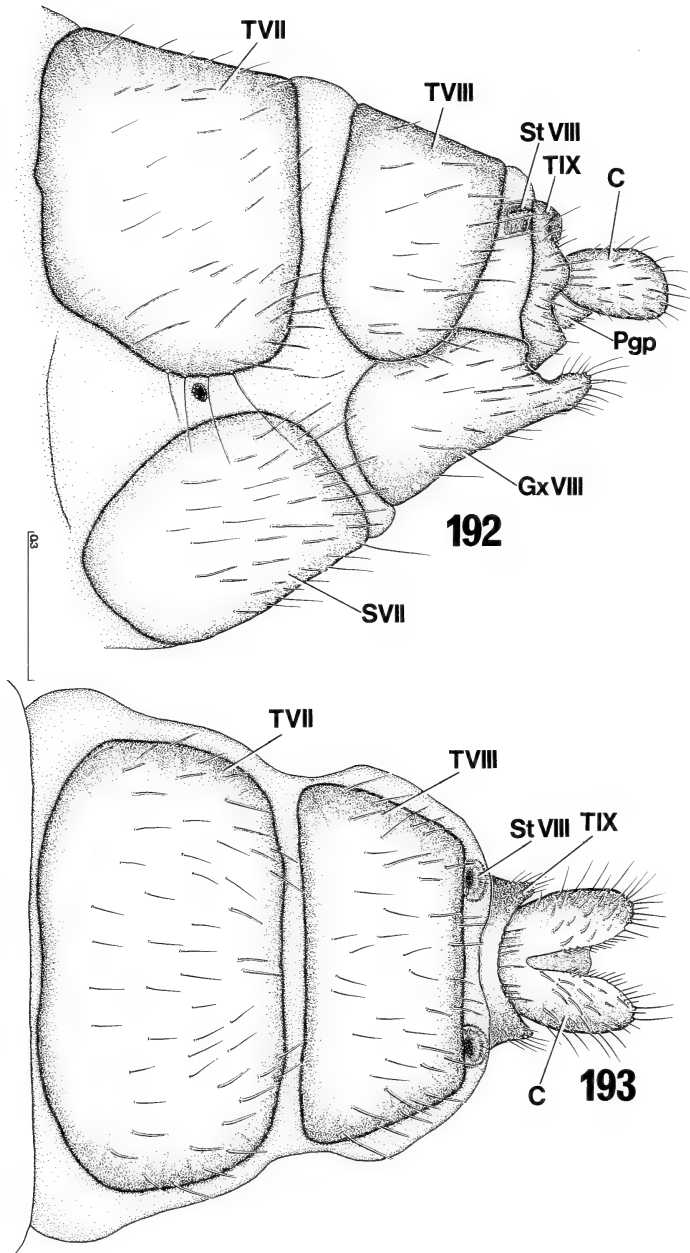
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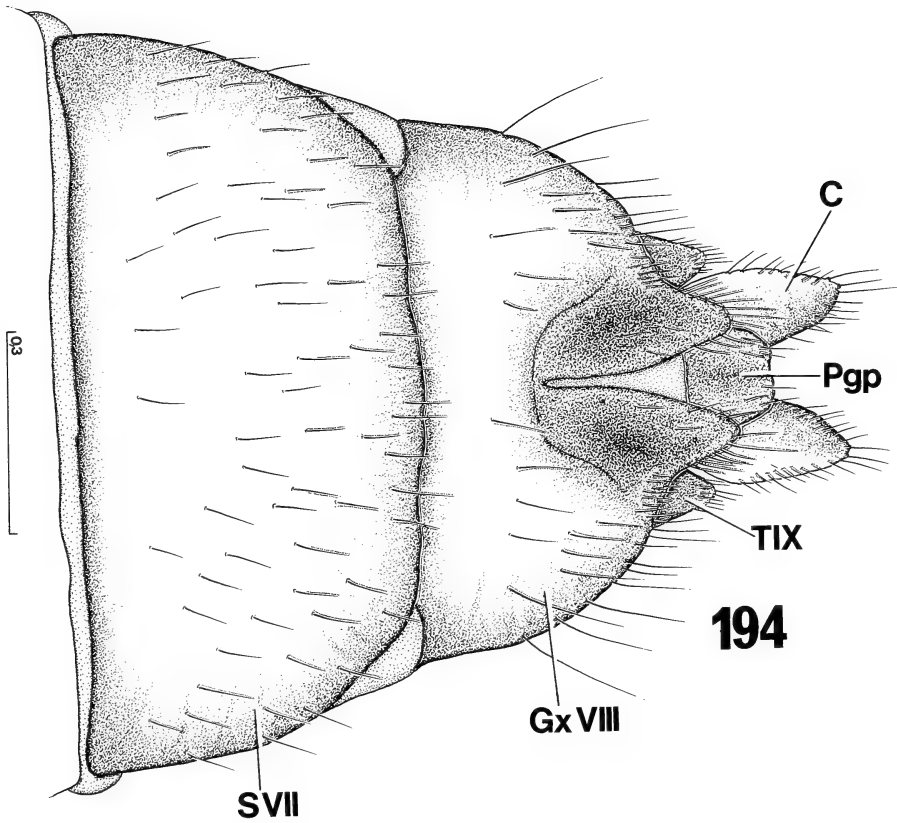
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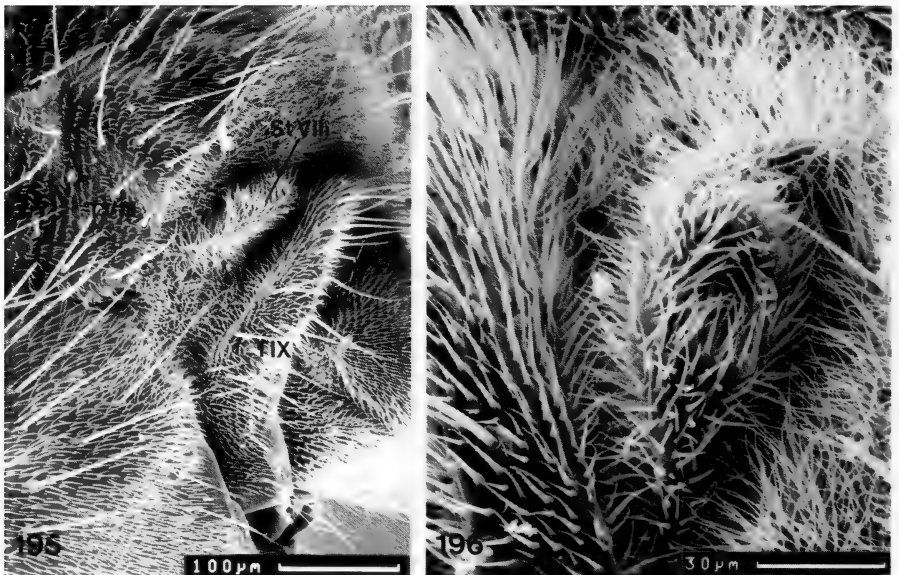
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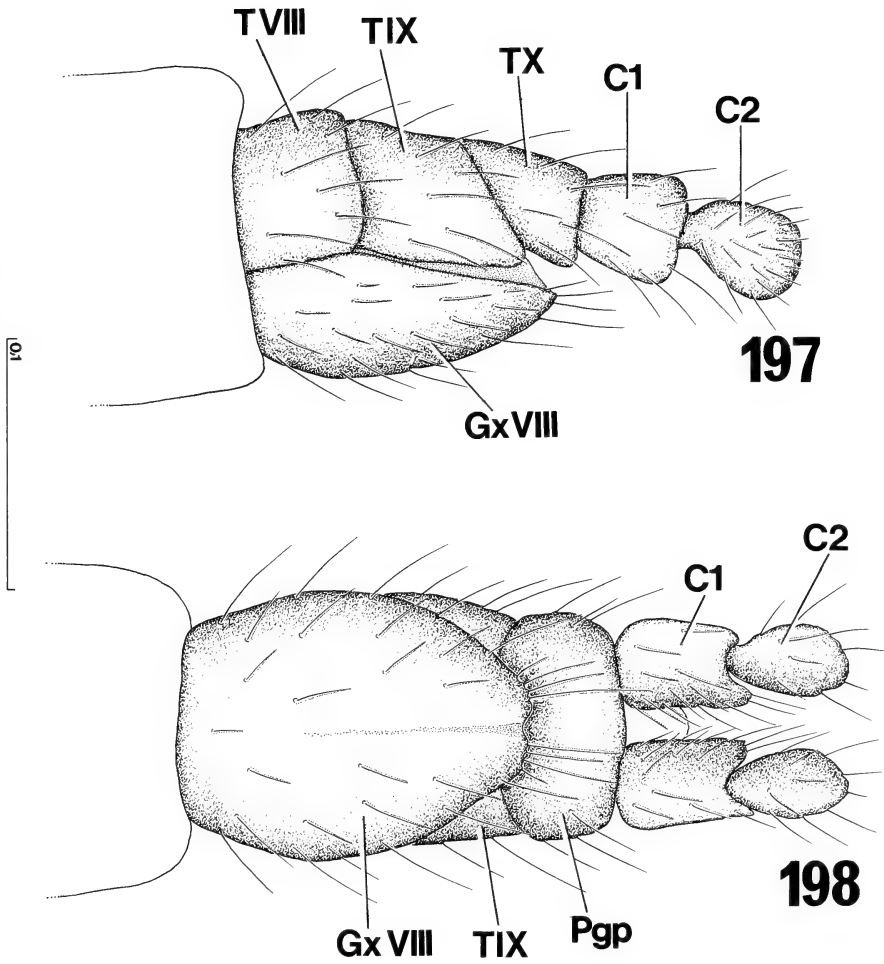
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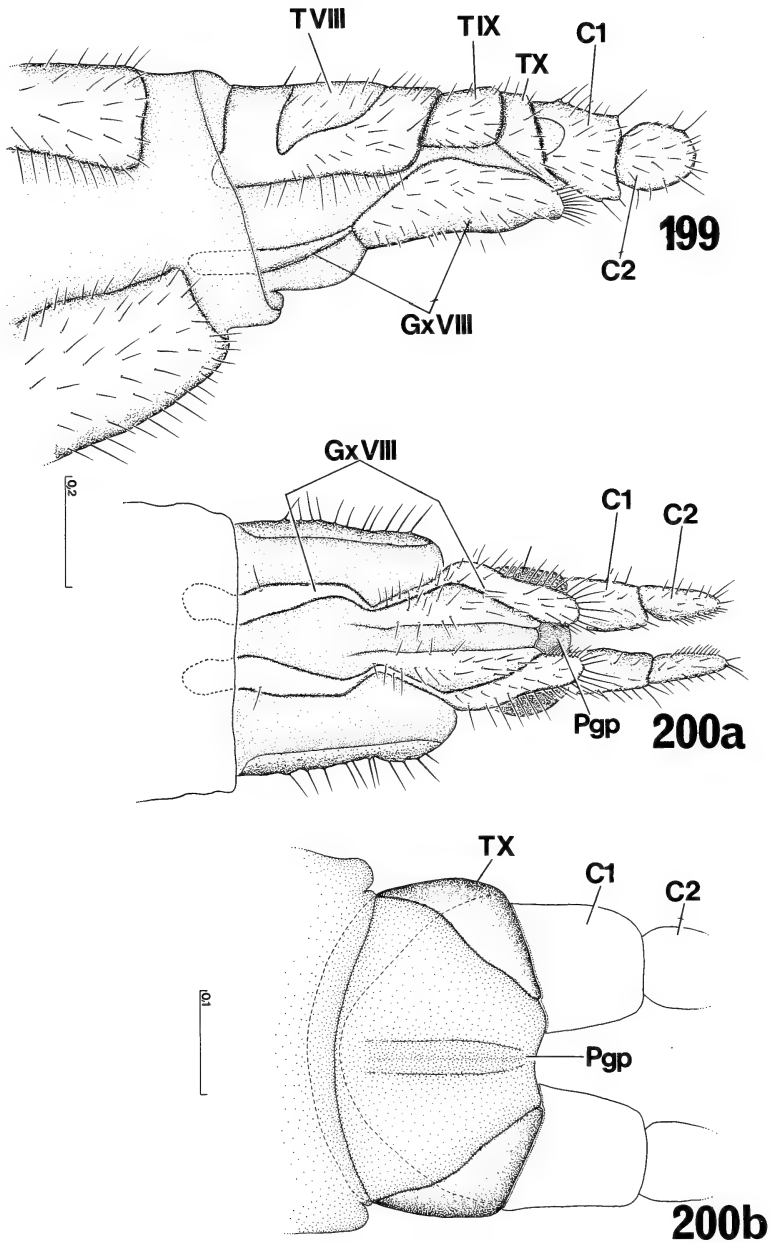
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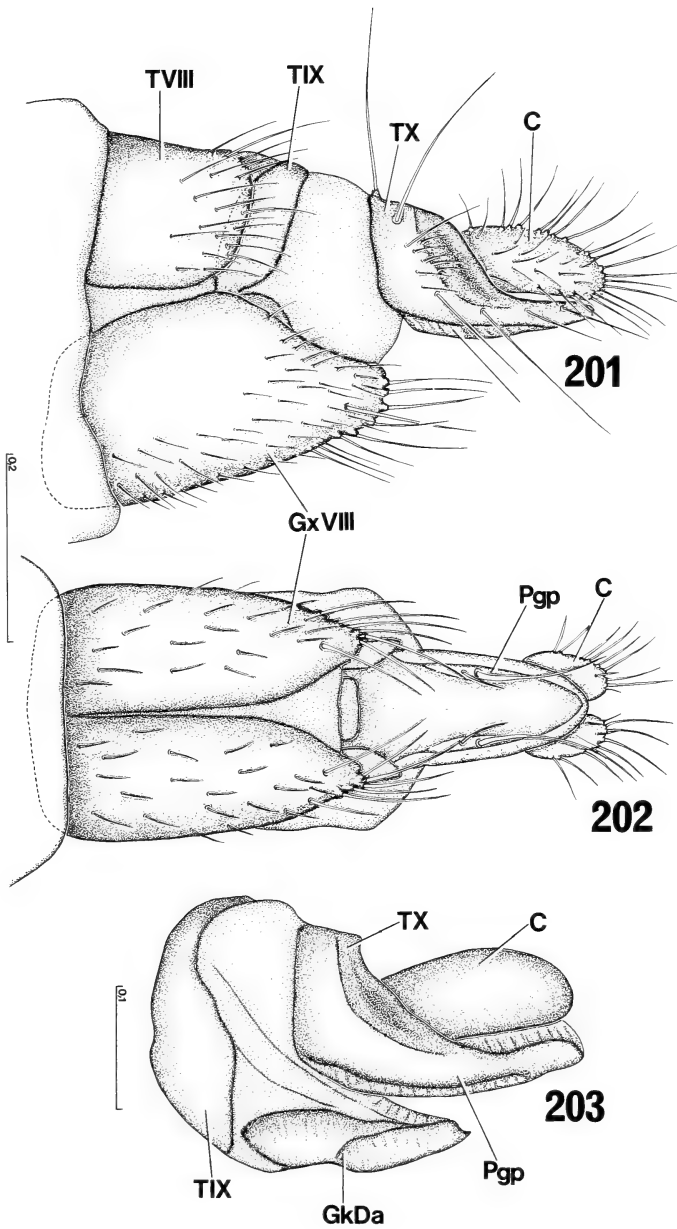
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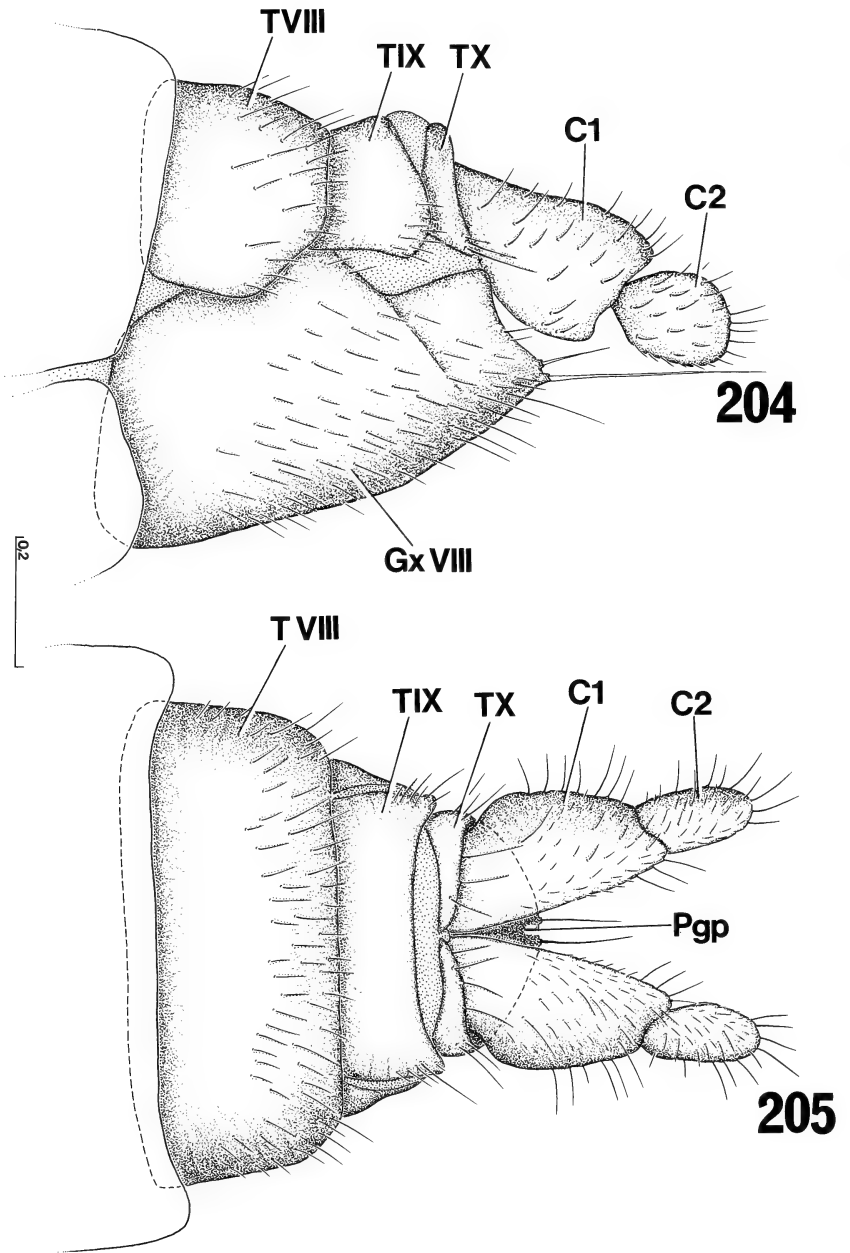
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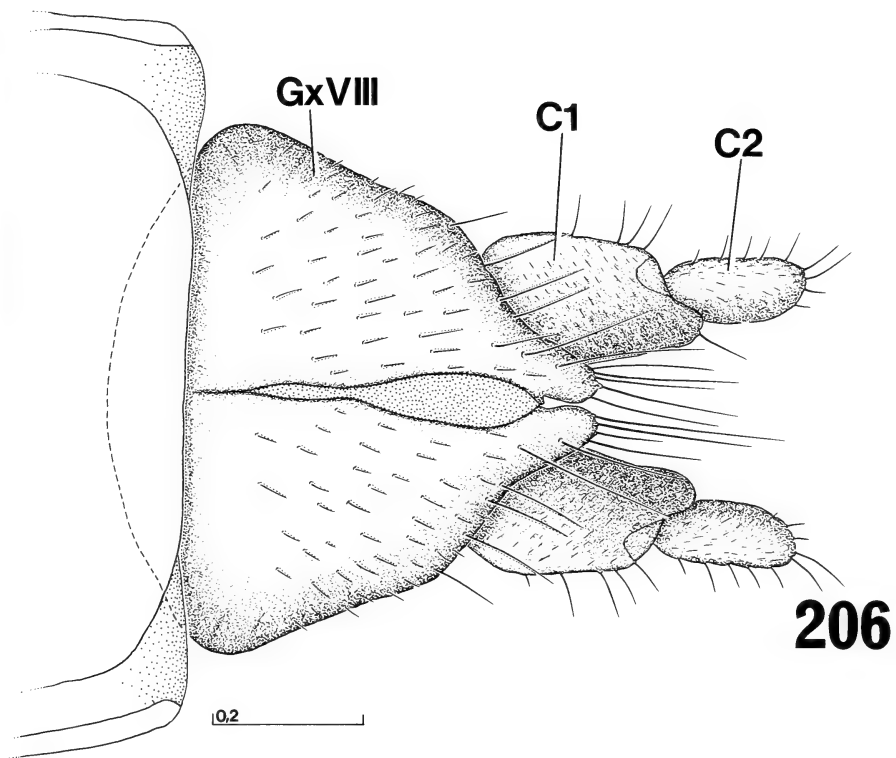
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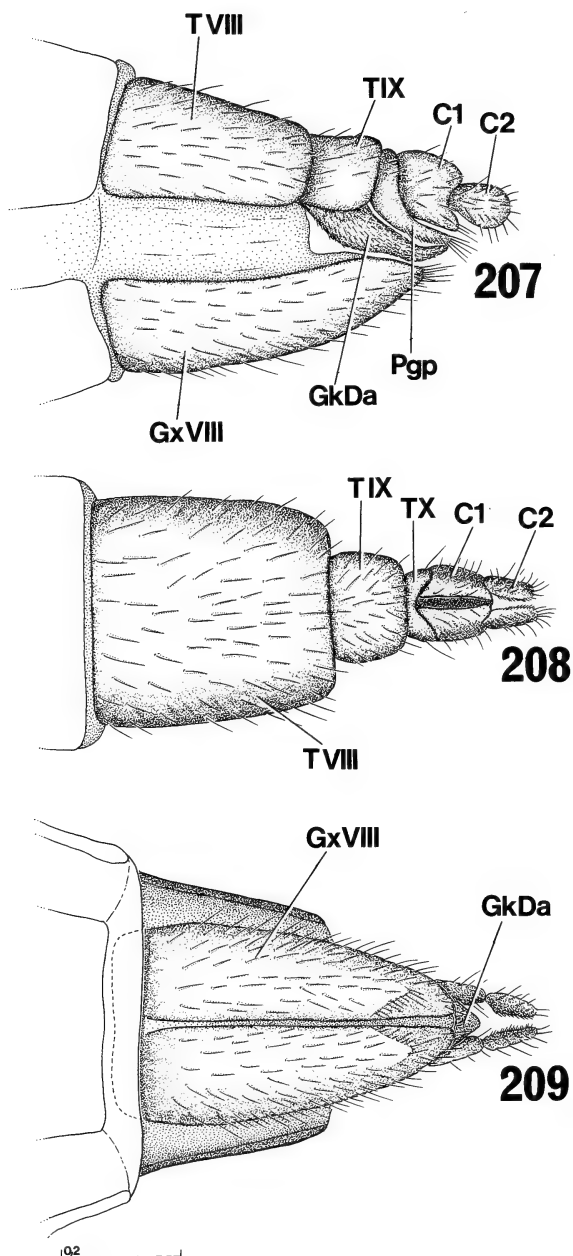
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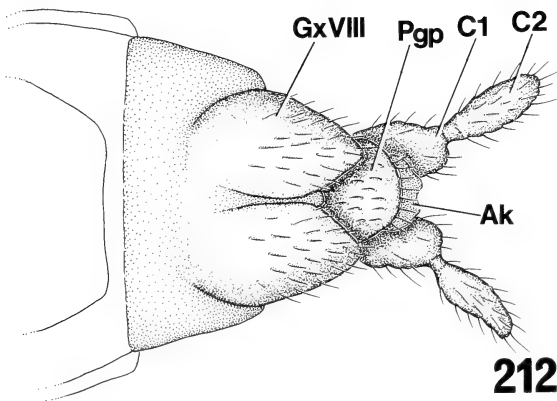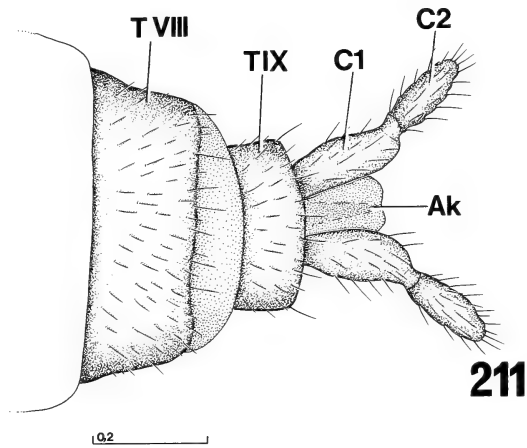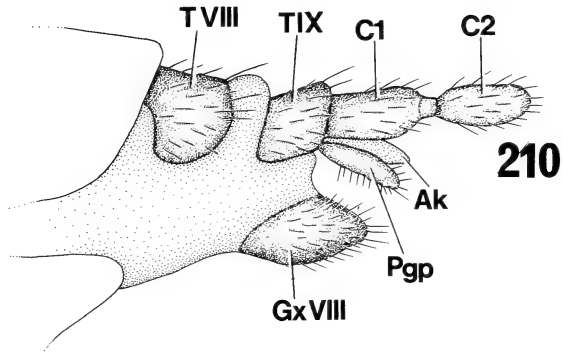
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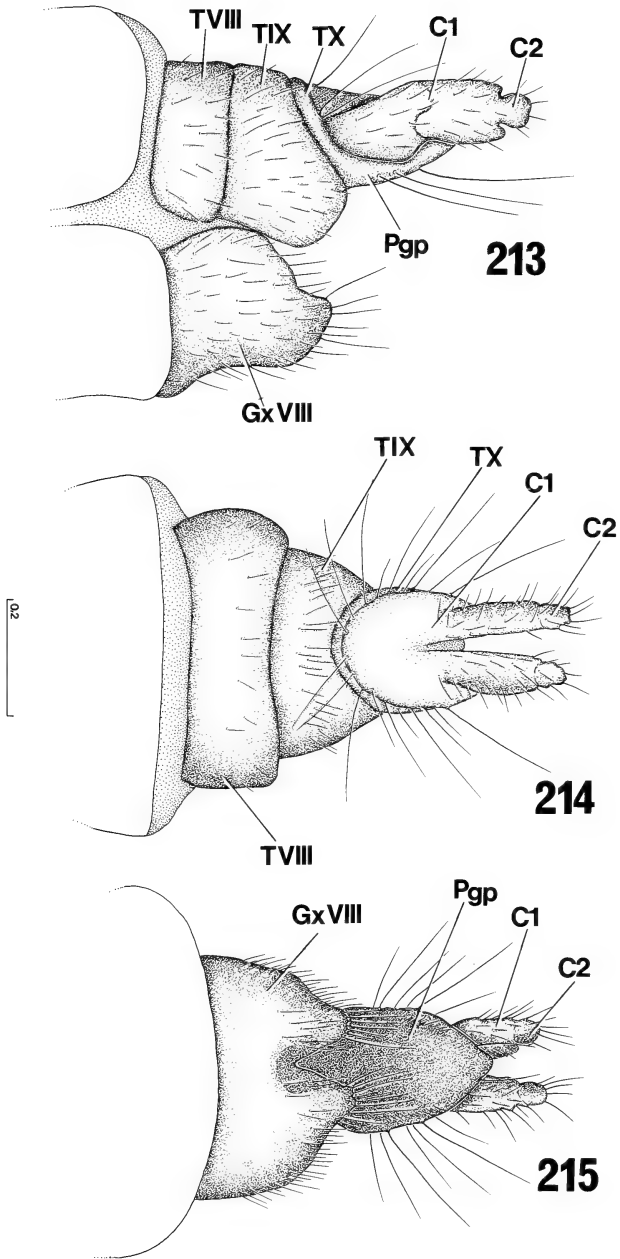
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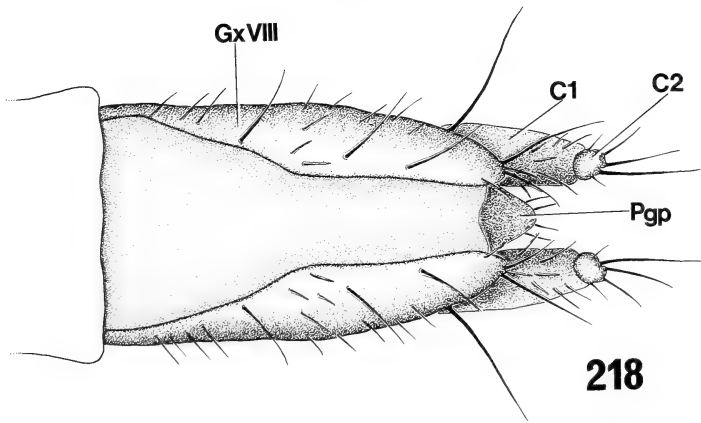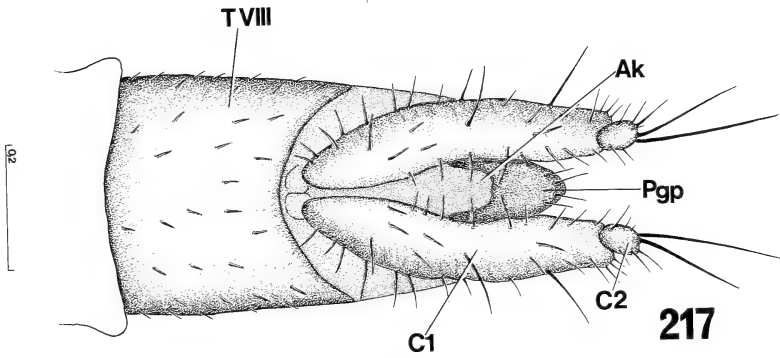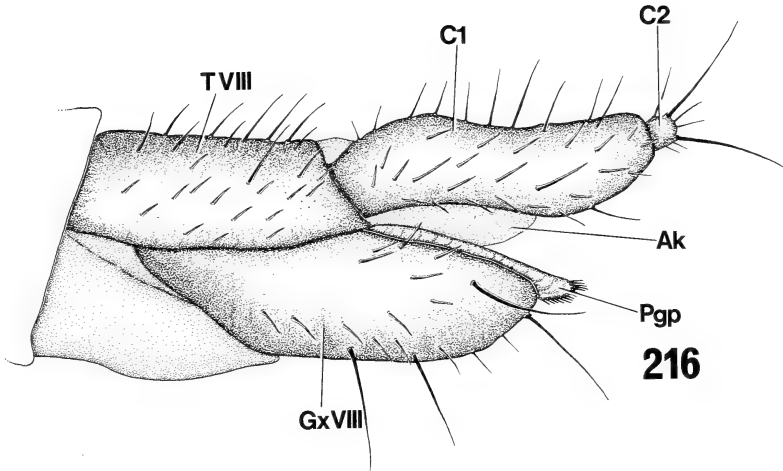
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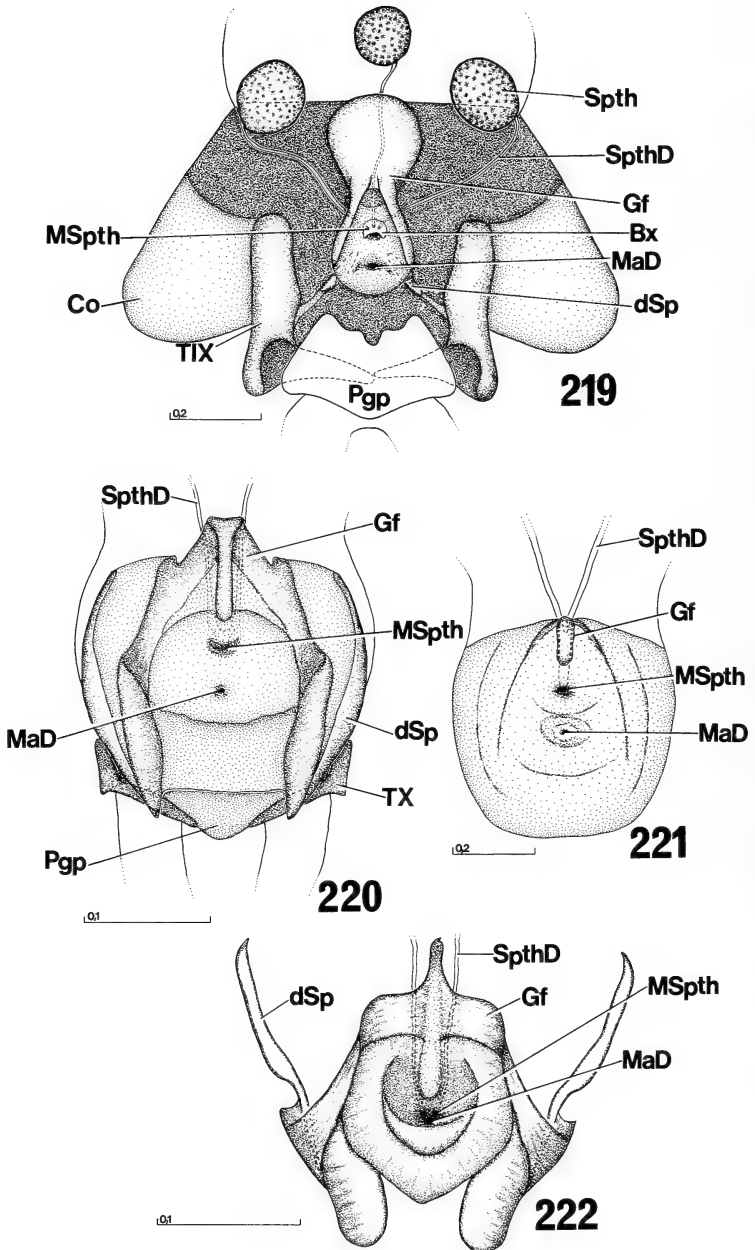
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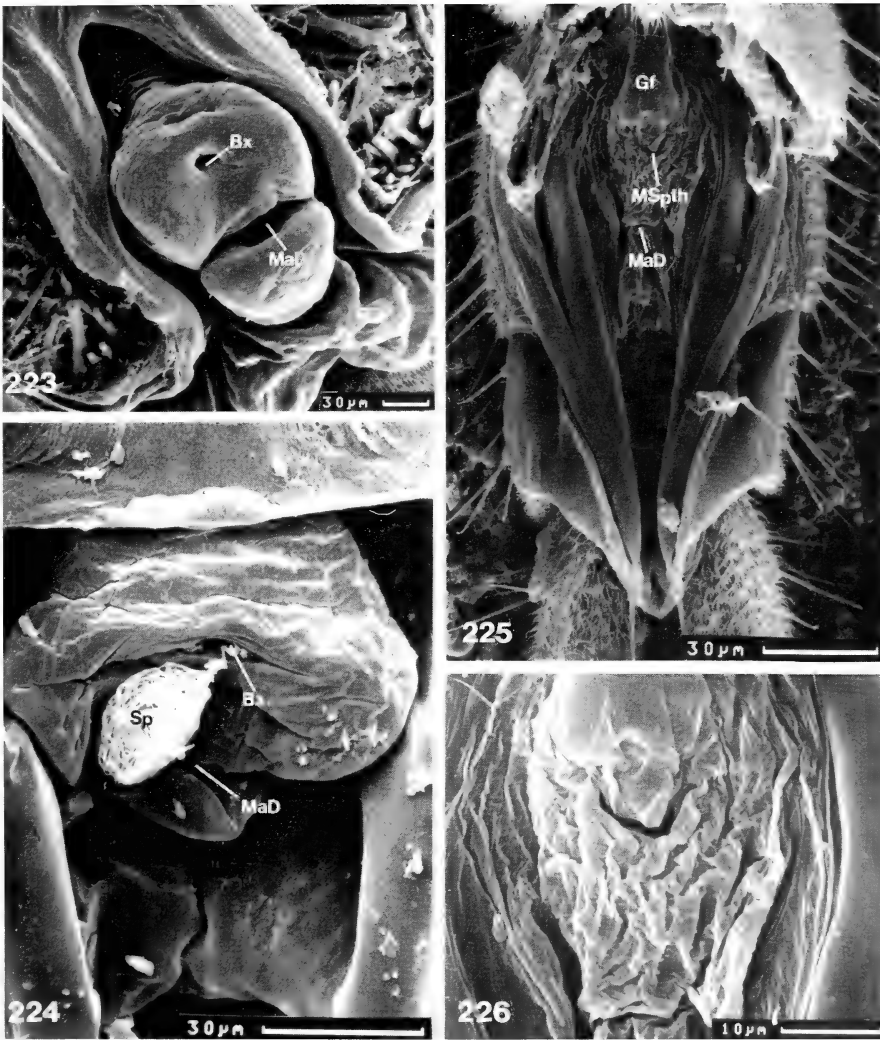
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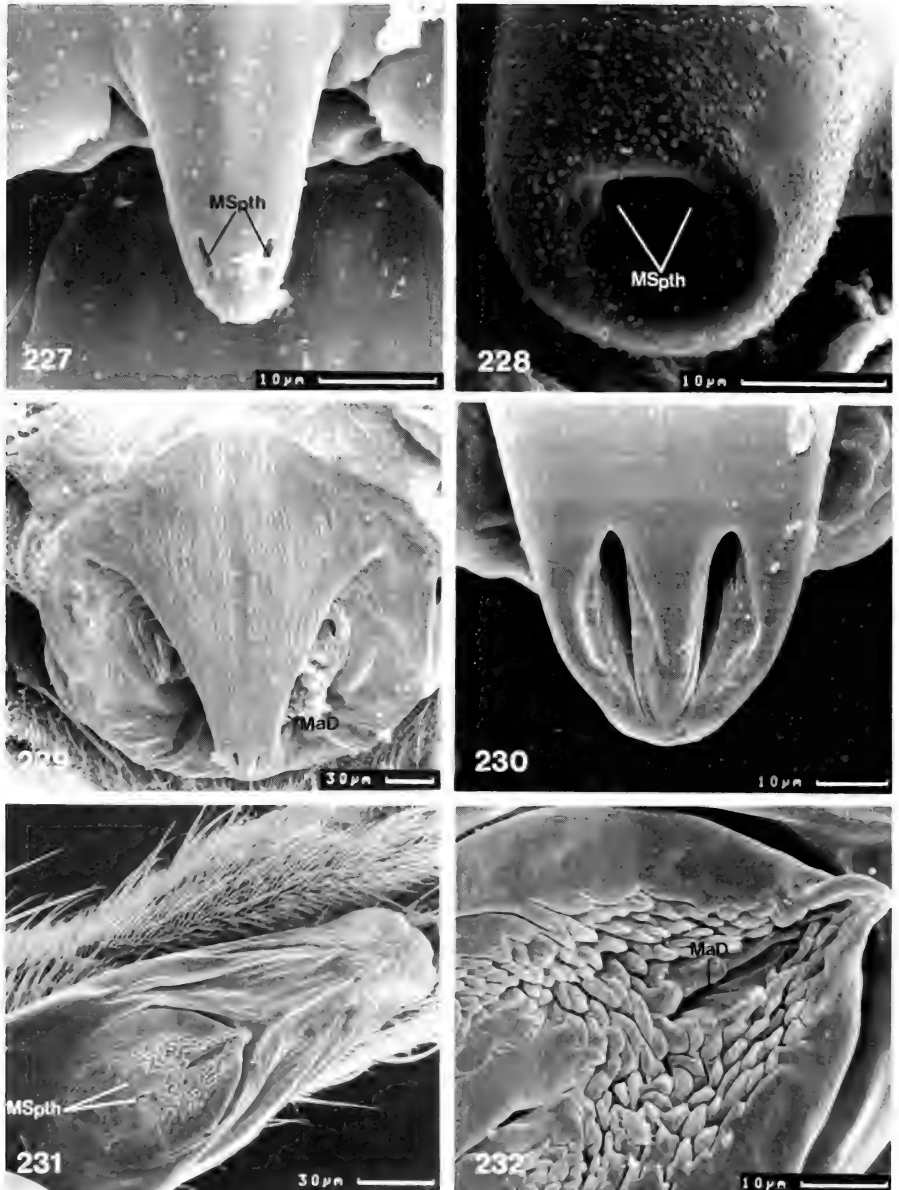
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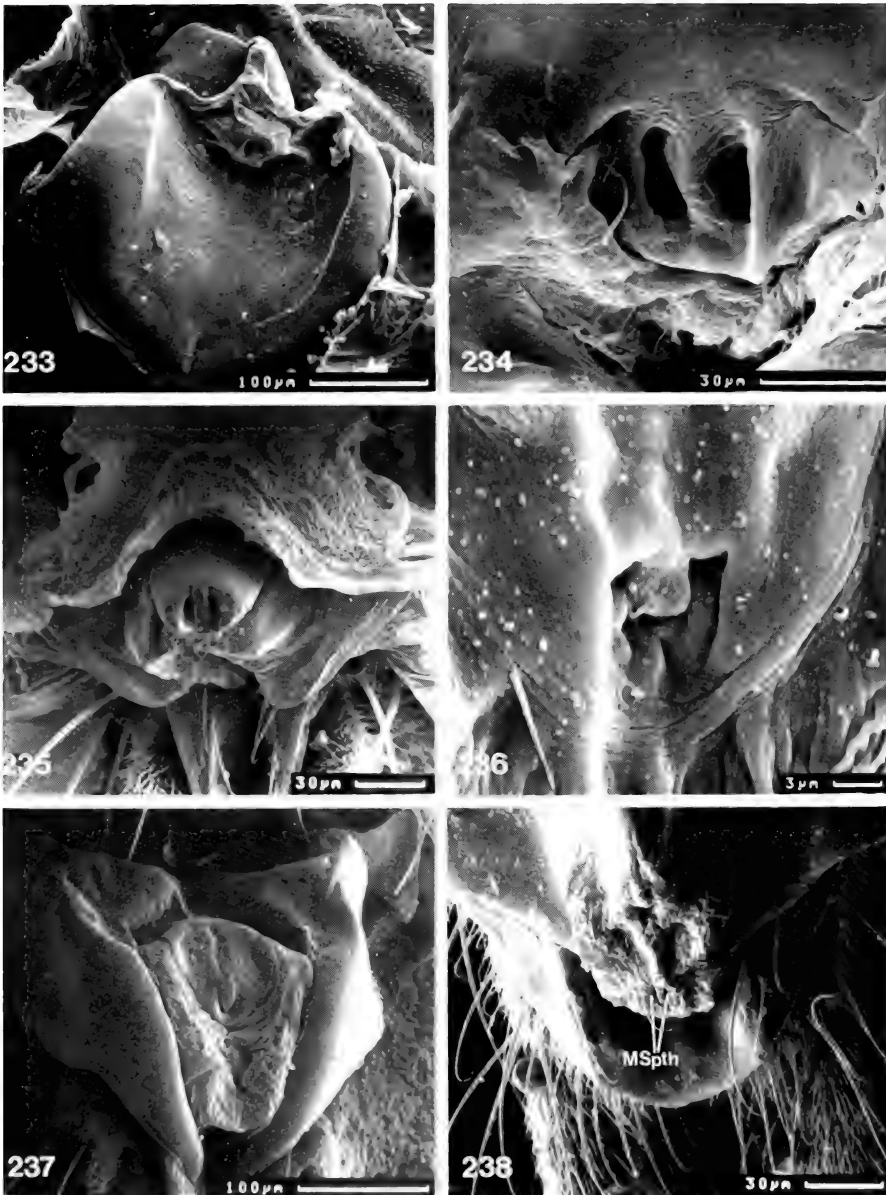
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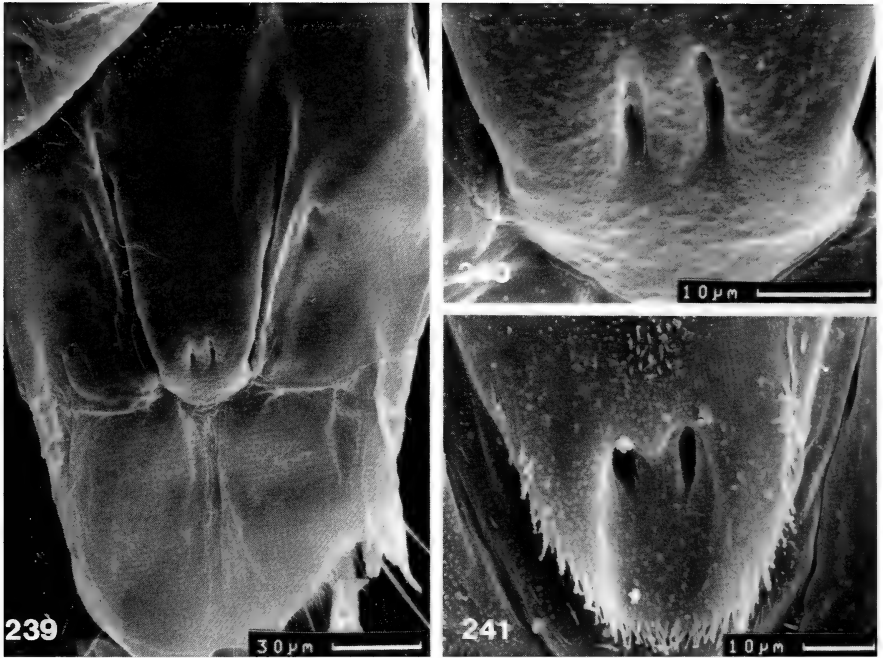
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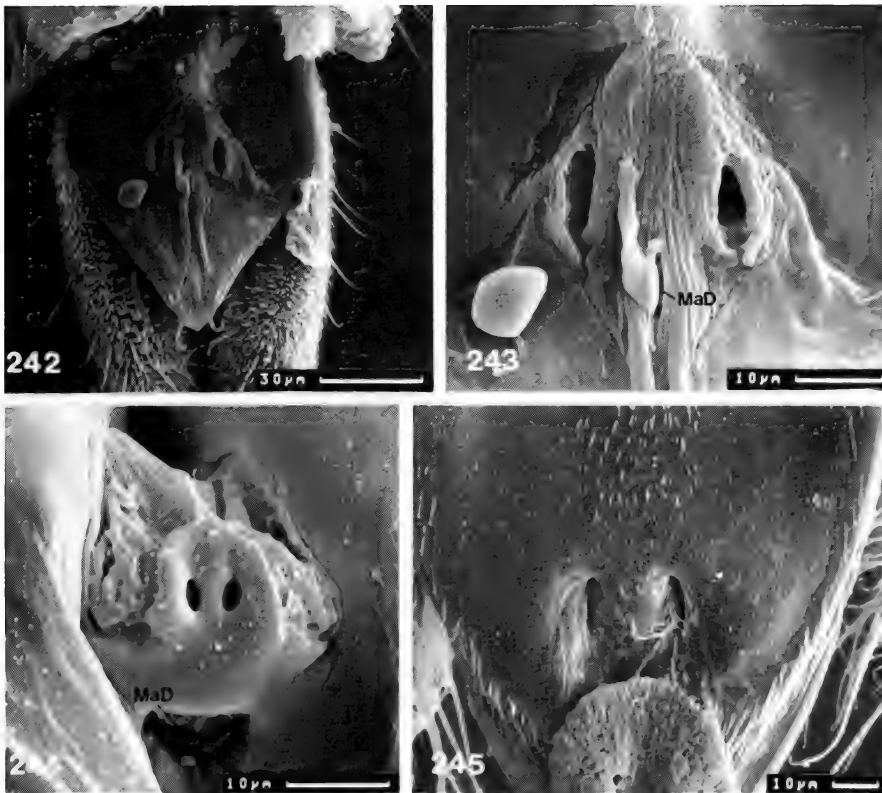
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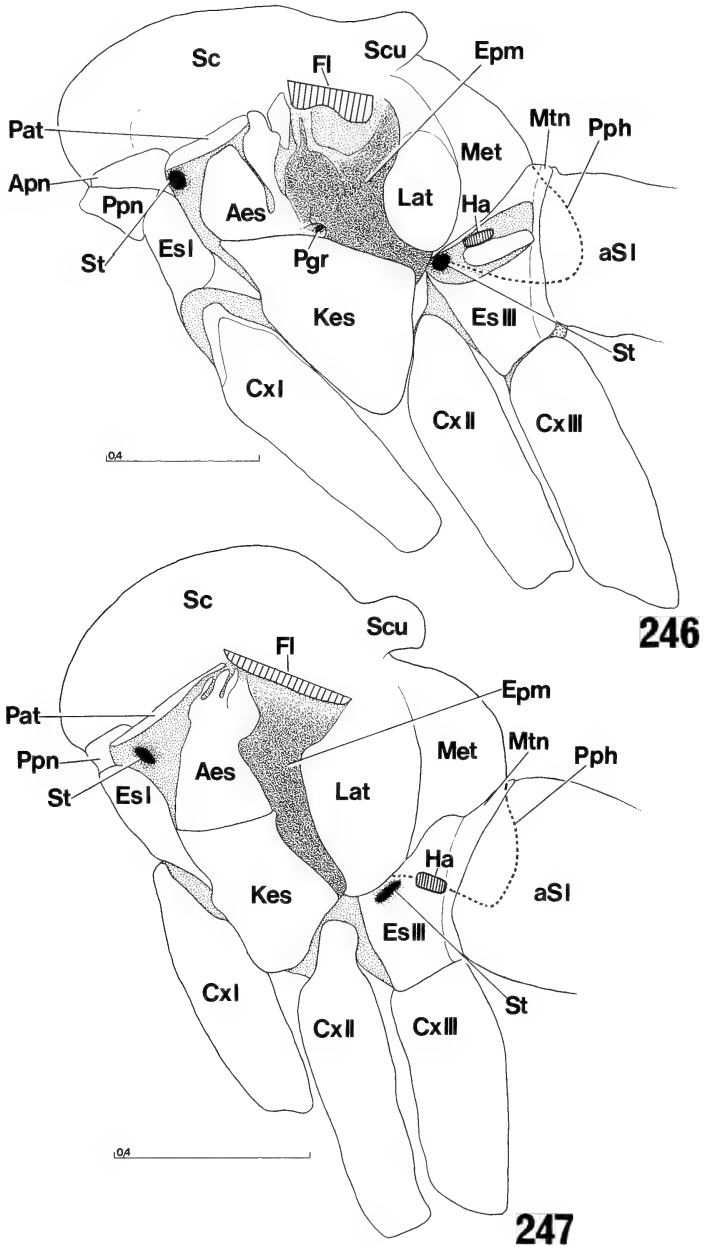
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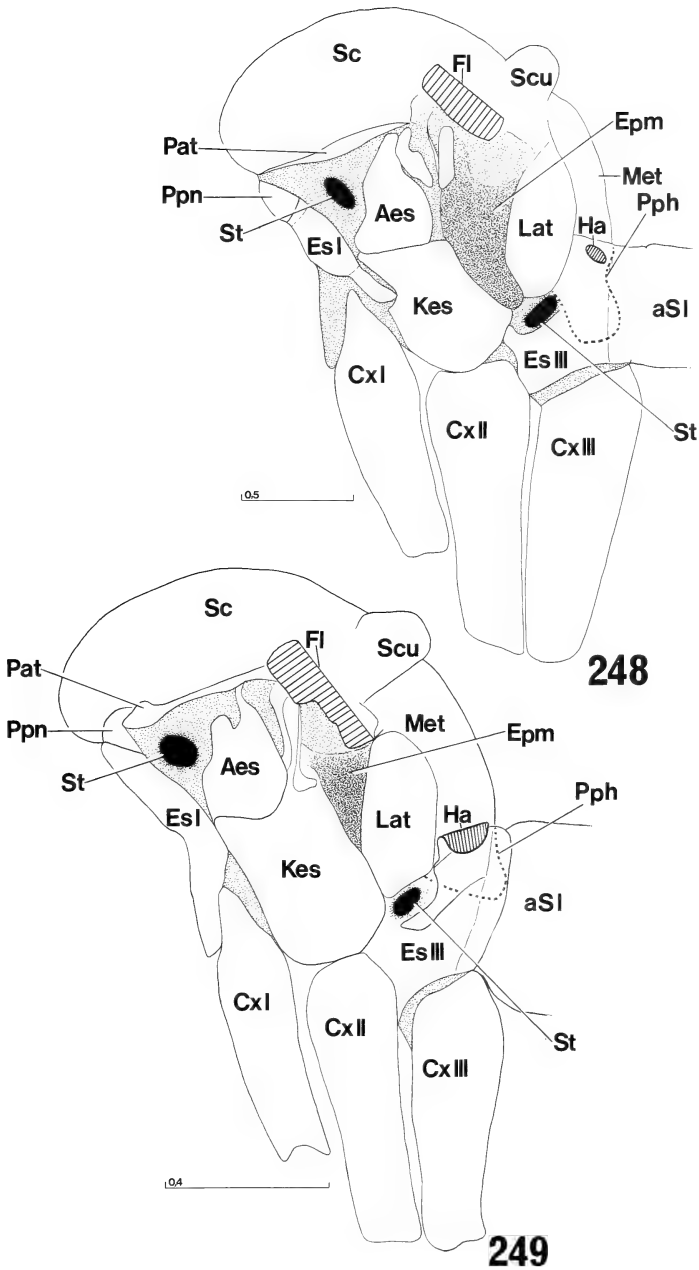
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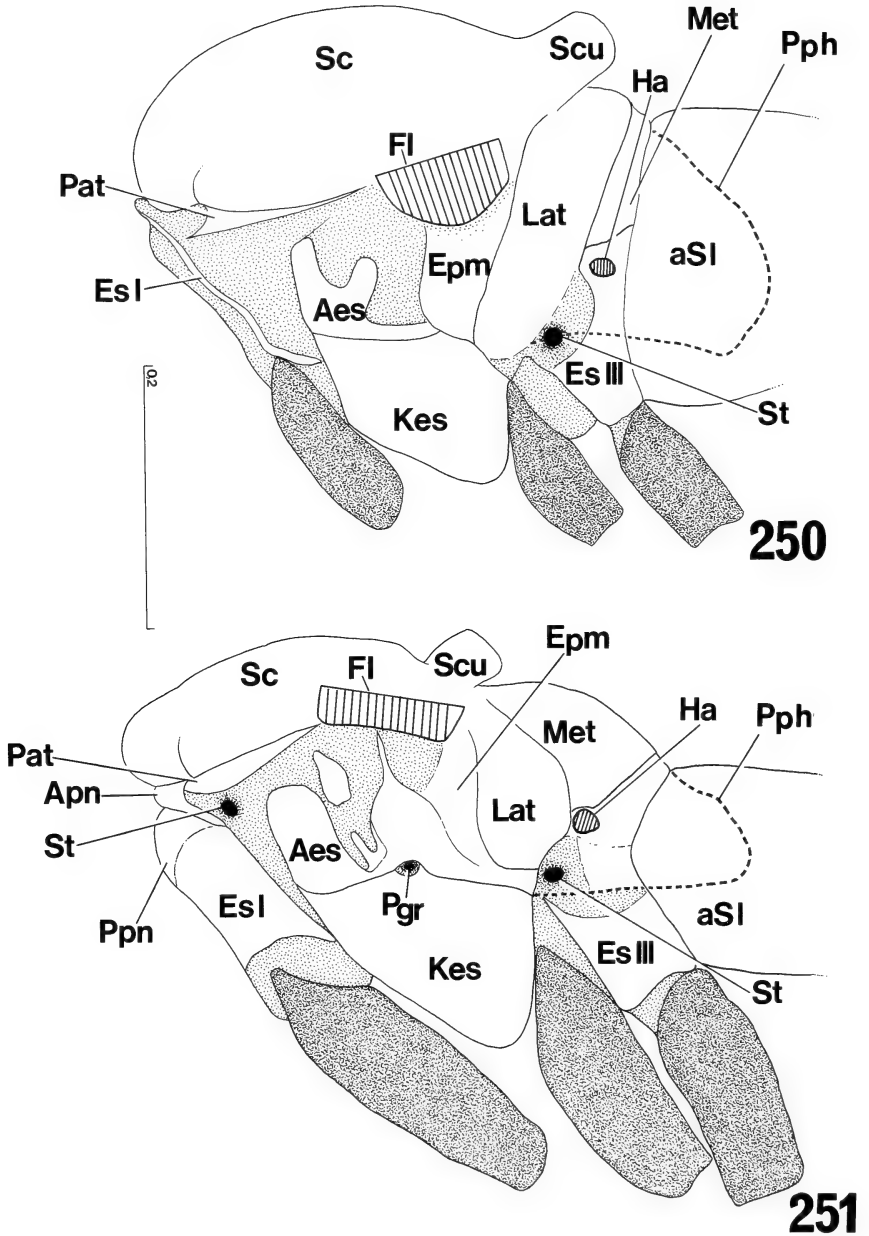
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Fe

Tb

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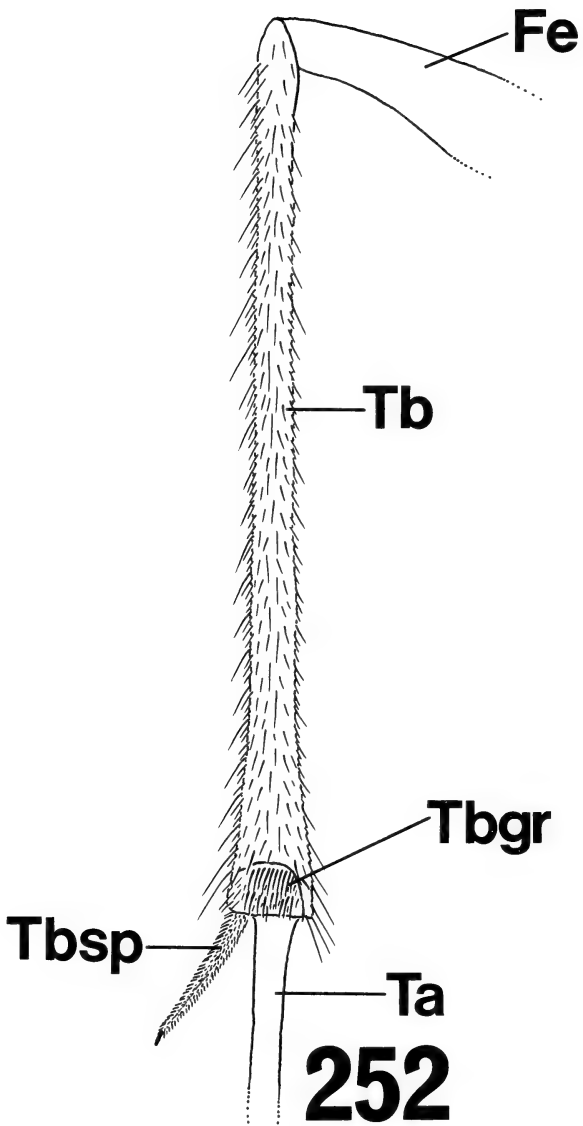
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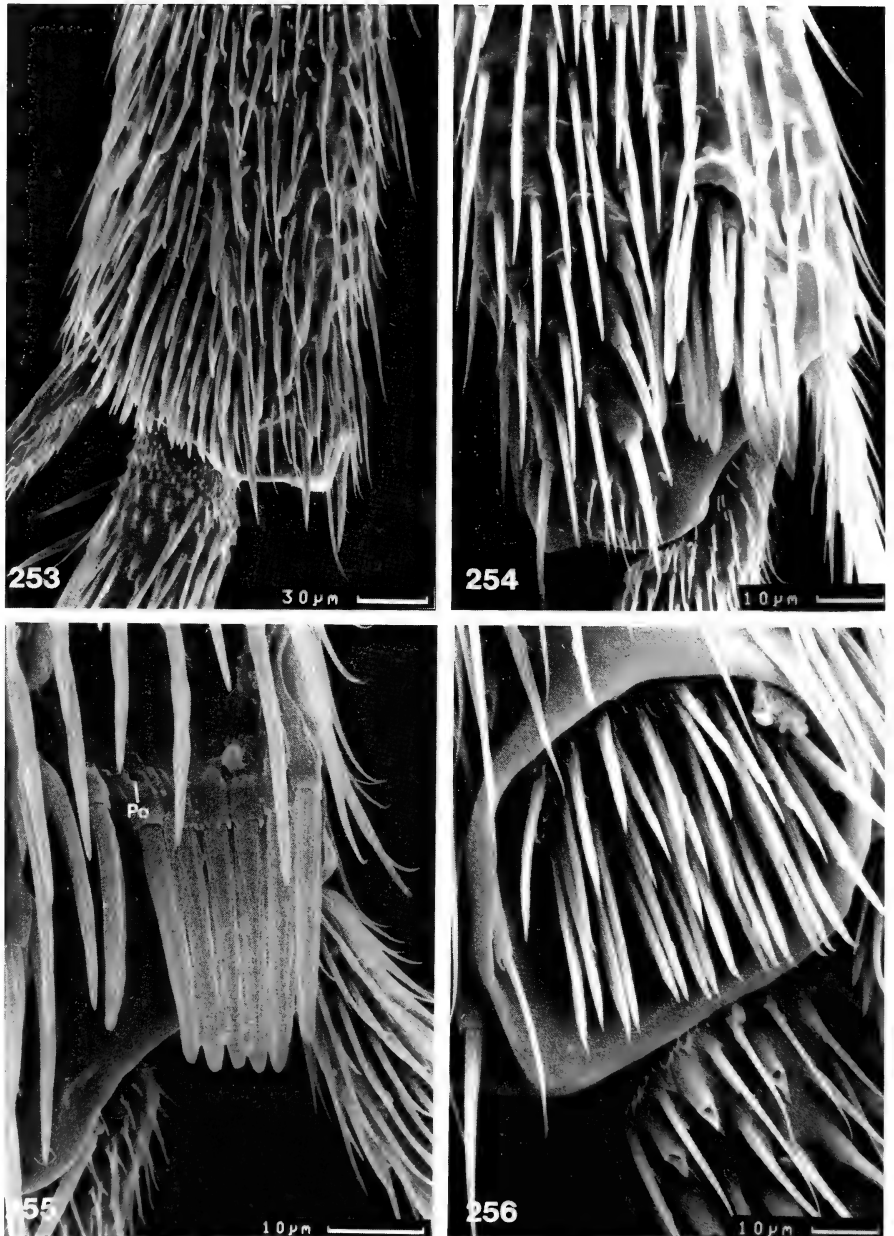
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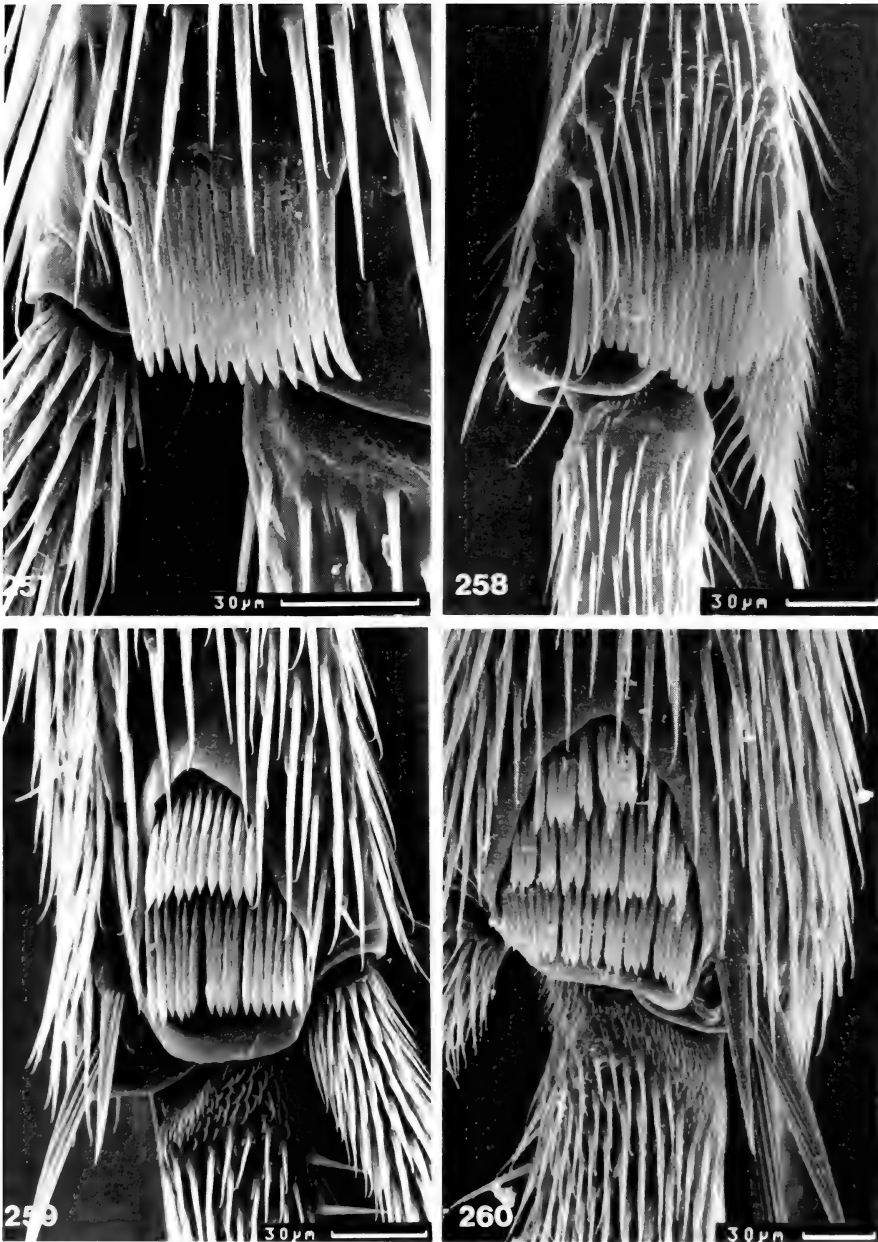
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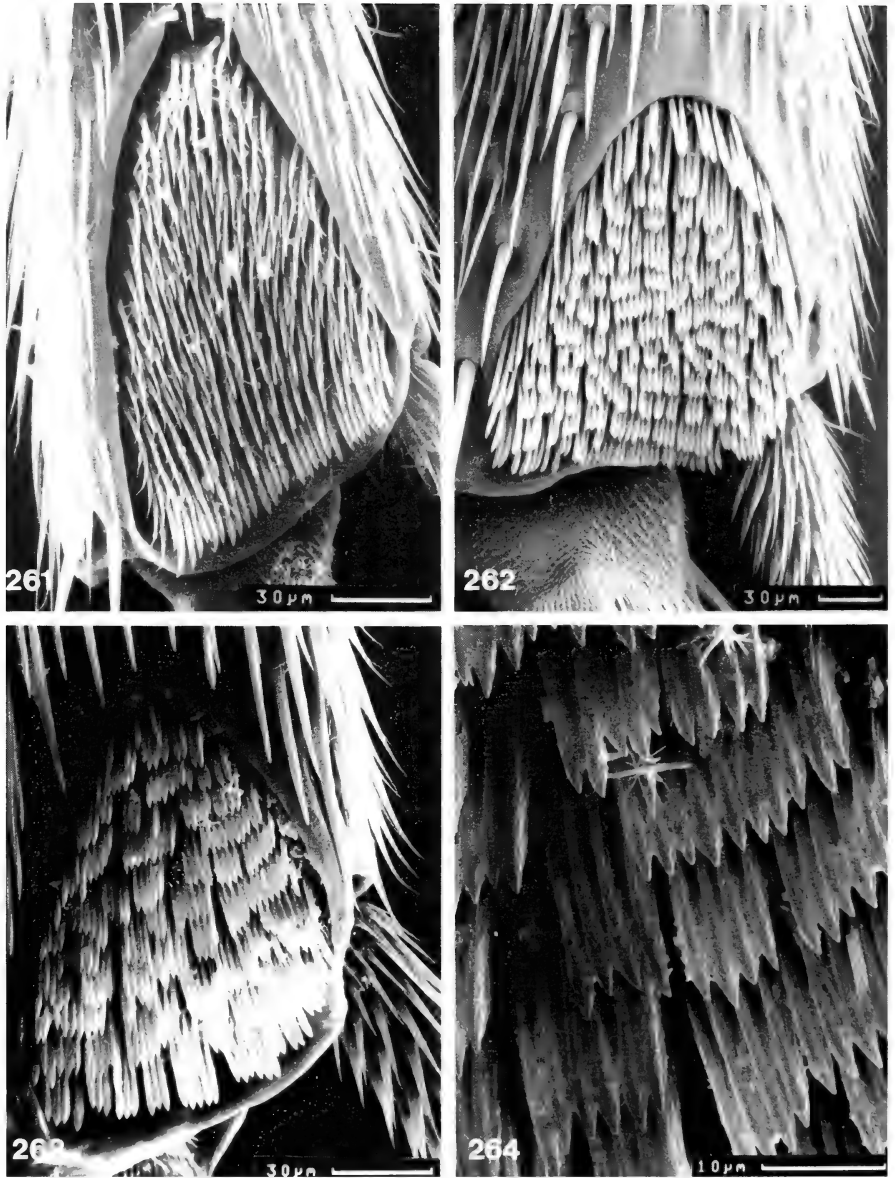
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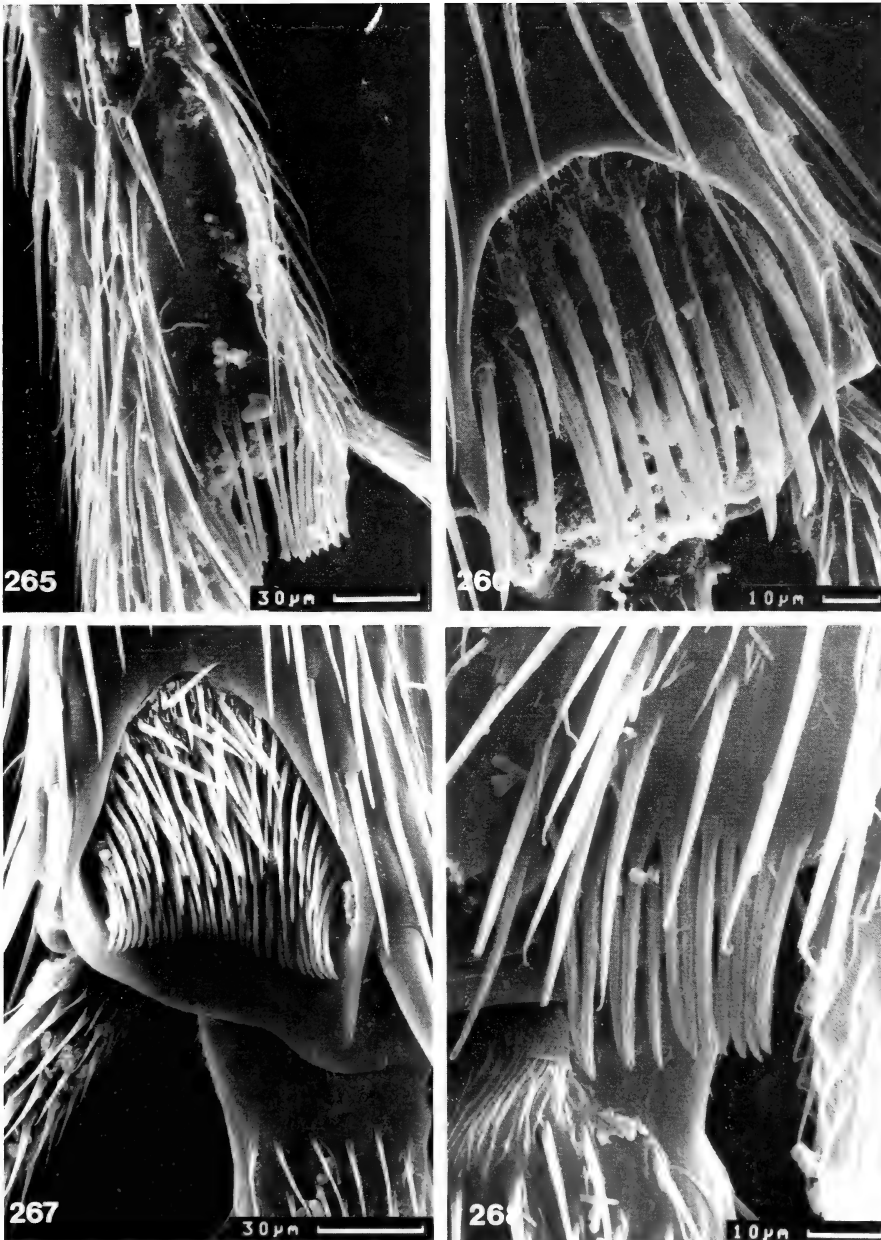
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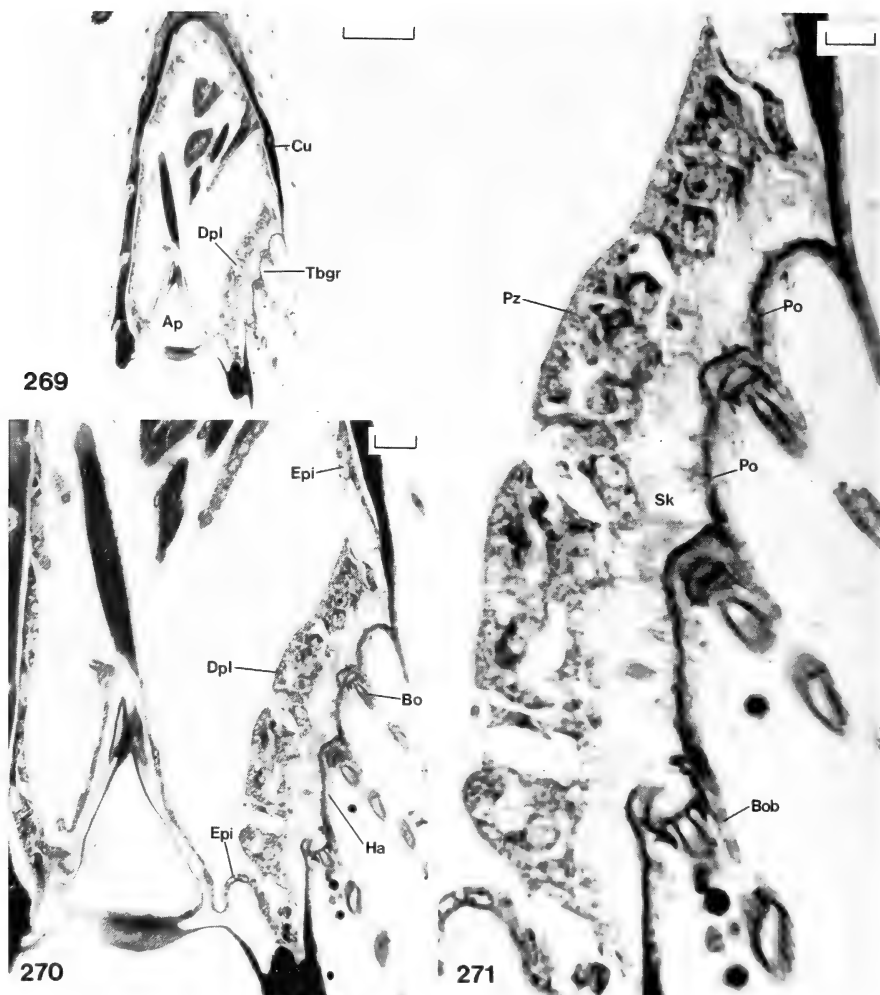
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