# The Present State of Knowledge of the Family Berothidae (Neuropteroidea: Planipennia)

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The Berothidae are a very small family of Planipennia which have unaccountably been neglected up to now, and of which our knowledge is rather unsatisfactory. This statement, as well as the title, indicates that the following article will not be a concise summary of "THE BEROTHIDAE" with comprehensive information, but rather a very generalized survey of the following aspects:

- o Important historical contributions to knowledge of the family;
- o our knowledge of the distribution, especially of genera;
- o available details on the biology (of a single species!); and, with emphasis on our own research and experience,
- o several problems of a taxonomic and systematic nature.

#### HISTORICAL REVIEW

The history of research on Berothidae began 132 years ago with the description of Hemerobius flavicornis by WALKER (1853). The nominate genus Berotha was erected seven years later in 1860, again by WALKER, for Berotha insolita WALKER from India. In 1908, the Berothidae were elevated to family rank by HANDLIRSCH. TILLYARD (1916) observed oviposition and the first instar larva of Spermophorella, and in 1947 GURNEY described first and third instar larvae of a Lomamyia, and established an association with termites and ants. With the discovery of the Rhachiberothinae in 1959, TJEDER enriched the family with members with raptorial legs! As a consequence, a discussion commenced on the relationship of the Rhachiberothinae and Mantispidae (Platymantispinae) which has not yet been resolved. Much later, fossil berothids with raptorial legs were discovered by SCHLÜTER in 1978 and by WHALLEY in 1980. In 1967 MacLEOD and ADAMS proposed a new classification of the family which is still effective. In 1968 C.A. TAUBER and M.J. TAUBER succeeded in rearing all three larval instars of Lomanyia latipennis CAR-PENTER, thereby elucidating the first complete life-cycle within the family. In 1981 JOHNSON and HAGEN discovered an aggressive allomone produced and utilized by berothid larvae to attack termites.

The taxonomic spade-work of the recent past has facilitated a succession of generic revisions. Our own expeditions to Australia and Africa, especially aimed at Berothidae, have provided a new basis for future research and understanding of the family.

## PRESENT STATE OF CLASSIFICATION AND TAXONOMY

As mentioned initially, we are dealing with a very small family. Up to now, 94 species have been described. After various transactions on the current systematic account, descriptions of new species, withdrawing of species as synonyms, transferring of species e.g. to Dilaridae, etc., the latest total is 78 species (see table 1). They are grouped, according to MacLEOD & ADAMS (1967), into four subfamilies:

The Cyrenoberothinae with only one species from South America, the Rhachiberothinae with five species in two genera occurring in South Africa, the Nosybinae with seven congeneric species confined to Africa, and the Berothinae with the bulk of species, namely 65, represented on all continents. These four subfamilies are, at least, a good working-hypothesis, but the Berothinae are a rather heterogeneous assemblage, and possibly not monophyletic. Most species are currently known from Africa. Whether this phenomenon has biogeographic reasons or is due to intensive collecting, remains to be seen.

Of 29 genera hitherto described, 18 have proved to be valid (see tables 2 and 3). The genera Cyrenoberotha MacLEOD & ADAMS (1967) (Cyrenoberothinae), Rhachiberotha TJEDER (1959), and Mucroberotha TJEDER (1959) (Rhachiberothinae) have been defined by modern criteria. The genus Nosybus NAVAS (Nosybinae) was revised quite recently (U. ASPOCK & H. ASPOCK 1983), and several genera of the Berothinae were similarly elaborated. Berotha WALKER had, until recently, been misunderstood and became a conglomerate of disparate species of the old world, including Australia! It was clarified and reduced to a few species from the oriental region (U. ASPOCK 1983, U. ASPOCK & H. ASPOCK 1981b). Asadeteva U. ASPOCK & H. ASPOCK was erected recently on modern criteria (U. ASPOCK & H. ASPOCK 1981b). The revision of the hitherto monotypic Sphaeroberotha NAVAS has led to a substantial enlargement of the genus and to the conclusion that Sphaeroberotha NAVAS is a junior synonym of Nodalla NAVAS. Unfortunately, it has not been possible to study the type of Nodalla aegyptiaca NAVAS despite repeated efforts, so, in order to make certain, the synonymy of Sphaeroberotha has had to be postponed (U. ASPOCK & H. ASPOCK 1984a). The Australian Stenobiella TILLYARD

Subfamily	Approximate number of recognized species	Number of valid genera	Europe	Africa	Madagascar	Asia	Indomalayan Archipelagos	Australia	New Zealand	Pacific Islands	North America	Central America and Caribbean	South America
CYRENOBEROTHINAE	1	1											l
RHACHIBEROTHINAE	5	2		5									
NOSYBINAE	7	1		7									
BEROTHINAE	65	14	2	18	2	15	3	20	1	1	10	2	3
	78	18	2	30	2	15	3	20	1	1	10	2	4

Table 1. Numbers of species and genera and distribution of the subfamilies of Berothidae.

Genus	Approximate number of recognized species	Europe	Africa	Madagascar	Asia	Indomalayan Archipelagos	Australia	New Zealand	Pacific Islands	North America	Central America and Caribbean	South America
Cyrenoberotha	1						,					•
Rhachiberotha	2		•									
Mucroberotha ,	3											
Nosybus	7											
Berotha	4					•						
Sphaeroberotha	8											
Asadeteva	2				•							
Stenobiella	10						•					
Lekrugeria	2				•							
Spermophorella	3											
Isoscelipteron	7	•			•				•			
Podallea	10			•								
Lomamyia	12											
Naizema	2											
Trichoma	1						•					
Trichoberotha	2						•					
Protobiella	1							•				
Austroberothella	1						•					

Table 2. Numbers of species and distribution of valid genera of Berothidae.

has recently been enlarged by a number of new species (U. ASPÖCK & H. ASPÖCK 1984b). The definite revision and characterization, however, is the subject of a forthcoming paper. The monotypic Barrowiella SMITHERS 1984 from the Barrow Islands (Western Australia) resembles Stenobiella with regard to the d genitalia, but whether the establishment of a separate genus based merely on differing crossveins is justified, seems rather doubtful. The study of Lekrugeria NAVAS is in preparation. The revisions of Isoscelipteron COSTA, and Podallea NAVAS (U. ASPÖCK & H. ASPÖCK 1980, 1981a, b) have provided new characterizations of these striking taxa which possess the most complicated internal d genital structures within the Berothidae. Spermophorella TILLYARD, which will be revised in the near future, has surprisingly-proved to be an "initial stage" of the former ones, regarding d genitalia. Lomamyia BANKS is a long-established genus, well researched by

the study of numerous species (CARPENTER 1940), but lacks a recent treatment. Naizema NAVAS was redescribed according to modern criteria by MacLEOD & ADAMS in 1967. The similarity of wing venation between Trichoma TILLYARD and Trichoberotha HANDSCHIN, already diagnosed by HANDSCHIN himself, has now been ascertained, as is the case for the \$\delta\$, and in general also for the \$\oldsymbol{Q}\$ genitalia (HANDSCHIN 1935; U. ASPOCK & H. ASPOCK 1985). The only \$\oldsymbol{Q}\$ individual hitherto known from the monotypic genus Trichoma, is brachypterous. As this specimen does not appear to be deformed it is safe to assume that at least the species T. gracilipenne TILLYARD is normally brachypterous and possibly not a good flyer. The two monotypic genera Protobiella TILLYARD and Austroberothella U. ASPOCK & H. ASPOCK are known from females only, and because of the morphology of their genitalia they occupy a special position within the Berothinae. Their exact classification will depend on information on the still unknown males (U. ASPOCK & H. ASPOCK 1985).

# EXAMPLES OF GENITAL MORPHOLOGY AS ESSENTIAL CRITERIA IN DETERMINING SYSTEMATIC RELATIONSHIPS

Former genus concepts were based almost exclusively on the morphology (shape and venation) of wings. These and other distinctive eidonomic 1) characters, for example scale-like modified hairs on wings, thorax or coxae, coloration, etc. afford, at best, useful criteria for the taxonomy of species, but are insufficient for generic classification. The study of morphological characters of the genitalia has led to numerous amendments in the generic grouping of species, and culminated in exposing surprising relationships between eidonomically heterogeneous taxa. On the other hand, however, it should not be denied that similarities in the morphology of genitalia have also led to embarrassing affinities (e. g. to subfamilies of Mantispidae).

Cyrenoberotha MacLEOD & ADAMS (Fig. 1-2) (and with it the Cyrenoberothinae), represents without doubt an example of primitive  $\sigma$  genitalia among Berothidae (9th tergite and ectoproct separate!).

**Mucroberotha** TJEDER (Fig. 5-6), as a representative of the Rhachiberothinae, is extremely apomorphic, at least as far as the paramere-mediuncus complex is concerned (threadlike elongation). The resulting similarity to  $\sigma$  genitalia<sup>2)</sup> of **Trichoscelia signata** (HAGEN) (Platymantispinae) raises the question of the integration of Rhachiberothinae into the Berothidae, and whether or not it is a parallelism. For details see TJEDER 1959 and 1968.

Nosybus NAVAS (Fig. 3-4) (and consequently the Nosybinae) should be interpreted as advanced: the paramere-mediuncus complex is reduced to a rolled up bundle of fibres!

Within the Berothinae there are several evolutionary trends manifest in the & genitalia which cannot be classified in detail. Thus, for example, Lomamyia BANKS (Fig. 8-9) and Lekrugeria NAVAS (Fig. 7) resemble each other in the arrangement and simplicity of their & genitalia (paramere-mediuncus complex). Whether this is a (worthless) symplesiomorphy or an accidental similarity caused by "equalizing reduction", is still uncertain.

Naizema NAVAS (Fig. 10) is likewise difficult to classify with its coiled bundle of bristles. By comparison with Lekrugeria NAVAS and Lomamyia BANKS its paramere-mediuncus complex is certainly a derived one. Compared with Nosybus NAVAS, without doubt a non-related genus, the same structure seems to be a similar plesiomorphic initial stage.

<sup>1)</sup> eidonomic characters = morphological characters visible without dissection

<sup>2)</sup> in combination with raptorial legs and a sinus-shaped anterior median in the hindwing!

Genus	Taxonomic status							
Gendo	raxunumic status							
Cyrenoberotha McLEOD & ADAMS, 1967	valid							
Rhachiberotha TJEDER, 1959	valid							
Mucroberotha TJEDER, 1959	valid							
Nosybus NAVAS, 1910	valid							
Berotha WALKER, 1860	valid							
Sphaeroberotha NAVAS, 1930	probably syn. of <b>Nodalla</b>							
Nodalla NAVAS, 1926	probably valid							
Costachillea NAVAS, 1929	probably syn. of <b>Nodalla</b>							
Asadeteva U. A. & H. A., 1981	valid							
Stenobiella TILLYARD, 1916	valid							
Barrowiella SMITHERS, 1984	possibly syn. of Stenobiella							
Lekrugeria NAVAS, 1929	valid							
Spermophorella TILLYARD, 1916	valid							
Cycloberotha KRÜGER, 1922	syn. of Spermophorella							
Isoscelipteron COSTA, 1863	valid							
Dasypteryx STEIN, 1863	syn. of Isoscelipteron							
Acroberotha KRÜGER, 1922	syn. of <b>Isoscelipteron</b>							
Sisyrura NAVAS, 1905	probably syn. of Isoscelipteron							
Frawalkeria NAVAS, 1929	not yet reinvestigated							
Podallea NAVAS, 1936	valid							
Lomamyia BANKS, 1905	valid							
Naizema NAVAS, 1919	valid							
Espetera NAVAS, 1929	syn. of Naizema							
Trichoma TILLYARD, 1916	valid							
Trichoberotha HANDSCHIN, 1935	valid							
Protobiella TILLYARD, 1923	valid							
Austroberothella U. A. & H. A., 1985	valid							

Table 3. Taxonomic status of described genera of Berothidae.

Trichoma TILLYARD and Trichoberotha HANDSCHIN are closely related genera with a remarkable synapomorphic differentiation in the torulus (see Fig. 11). Other structures of the đ genitalia look rather primitive although they appear soft and reduced. The remarkable thing, however, is a striking similarity to the đ genitalia of Mantispinae (e. g. Mantispa ILLIGER) which may, no doubt, be seen as parallelism; nevertheless it cannot be satisfactorily interpreted as a whole (U. ASPÖCK & H. ASPÖCK 1985).

The genera Berotha WALKER, Sphaeroberotha NAVAS, Asadeteva U. ASPOCK & H. ASPOCK and Stenobiella TILLYARD (Fig. 12-15) correspond in the construction of their paramere-mediuncus-complex. They form the so-called "bow-bundle-type" (bundled fibres embracing a membrane), thereby most probably constituting a monophyletic group. The development of this structure from a simple plate with bristles (similar to those of Lekrugeria NAVAS or Lomamyia BANKS for instance) can easily be deduced theoretically, but is not yet proven. It should be especially emphasized that the genera Berotha WALKER, Sphaeroberotha NAVAS, Asadeteva U. ASPOCK & H. ASPOCK, and Stenobiella TILLYARD look very different phenetically (Fig. 19-22).

The genera **Spermophorella** TILLYARD, **Isoscelipteron** COSTA, and **Podallea** NAVAS (Fig. 16-18) form a very convincing monophyletic group presumably representing the sistergroup of the former. The bundle of bristles is fused into a compact bow framing a more or less coiled membrane with an extensively enlarged surface. In **Spermophorella** it is still rather simple; it shows the extreme degree of development in **Isoscelipteron** by culminating in a basket-like structure, and in **Podallea** it terminates in a series of frills.

The morphology of the female genitalia varies, too. The hypocaudae (Fig. 23), well known as a characteristic berothid feature, only occur within Berothinae. Not all species have hypocaudae as long as **Berotha** WALKER, they may be reduced or even almost obliterated, which implies a derived state. The lack of hypocaudae may, of course, also indicate a primitive state as for example in **Cyrenoberotha** MacLEOD & ADAMS. Nosybinae lack hypocaudae as well (Fig. 24), but with the elongation of the gonapophyses laterales a functionally equivalent structure is created as an apparatus which is supposed to serve as an ovipositor.

Protobiella TILLYARD and Austroberothella U. ASPOCK & H. ASPOCK (Fig. 25, 26) occupy an exceptional position within the Berothinae in the development of "pseudohypocaudae". These are finger-shaped appendages in the region of the 9th tergite+ectoproct. Irrespective of the appearance of the unknown males, it is extremely likely that these pseudohypocaudae are synapomorphic. A comparable situation exists only within the Rhachiberothinae, e.g. Mucroberotha TJEDER (Fig. 27). It only needs to be mentioned that the Rhachiberothinae are characterized by their modified raptorial forelegs and their sinuous anterior basal median in the hindwing. None of these features occur in Protobiella and Austroberothella, not even as vestiges. An interpretation of the pseudohypocaudae as synapomorphies of Rhachiberothinae on one hand, and Protobiella + Austroberothella on the other, would consequently mean that the latter had to be excluded from the Berothinae and put into a subfamily of its own. A similar speculative consideration would be whether the pseudohypocaudae are homologous to parts of the platymantispine ovipositor or not. The assumption of parallelism is, however, more convincing.

#### ECOLOGY AND BIOLOGY OF BEROTHIDAE

Generally speaking, very little is known about Berothidae at present. No one has any idea of how or where the adults of most species live, as they have almost exclusively been collected at light. This is true for the preimaginal stages to an even greater extent, as they are, with a single exception, almost unknown. But there is one species of which we know a great deal, namely Lomamyia latipennis CARPENTER. The complete life-cycle has been studied by TOSCHI (1964) and C. A. TAUBER & M. J. TAUBER (1968). The first and third instar larva is very mobile, carnivorous, with sucking and piercing mouthparts. The second instar, by contrast, is non-feeding, with short stubby legs. Incidentally, this modified second instar larva represents a remarkable similarity to the Mantispidae. The long suspected association of Berothidae with termites has been definitely verified. Lomamyia latipennis CARPENTER is a true termitophile of Reticulitermes hesperus BANKS (JOHNSON & HAGEN 1981). The larvae live freely among termites in their galleries without being attacked. The mobile first and third instar larvae produce an aggressive allomone

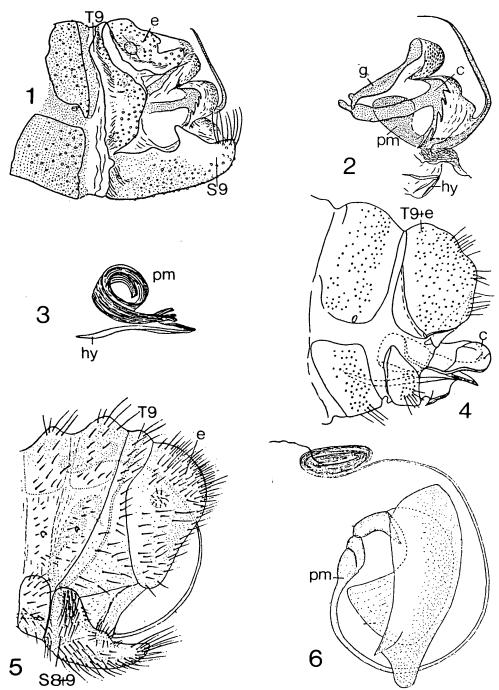


Fig. 1 - 6: Examples of d genitalia of different berothid genera. - 1 - 2: **Cyrenoberotha** penai MacLEOD & ADAMS; 1: genital segments, lateral; 2: genital sclerites, lateral. 3 - 4: **Nosybus navasi** BANKS; 3: paramere-mediuncus-complex and hypandrium internum, lateral; 4: genital segments, lateral. 5 - 6: Mucroberotha vesicaria TJED.; 5: genital segments, lateral; 6: genital sclerites, lateral. - Fig. 1 - 2 from MacLEOD & ADAMS, 1967; Fig. 3 - 4 from U. ASPÖCK & H. ASPÖCK, 1983; Fig. 5 - 6 from TJEDER, 1968.

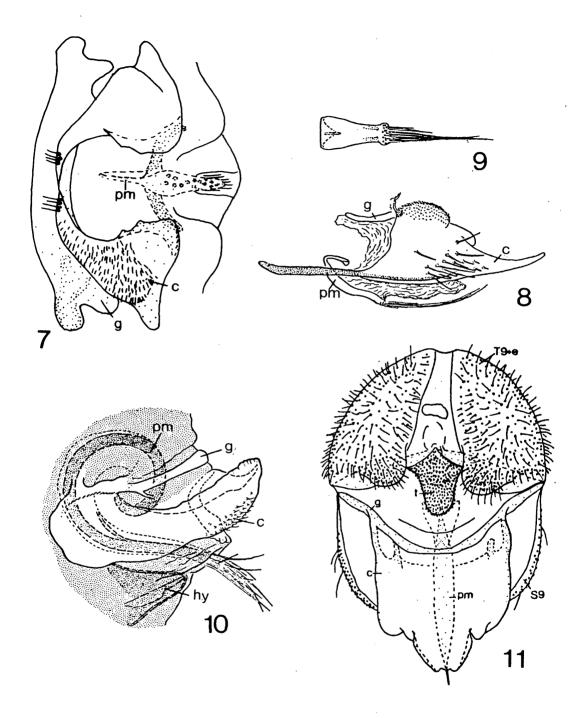


Fig. 7 - 11: Examples of d genitalia of different berothid genera. - 7: Lekrugeria lineata NAV., genital sclerites, caudal. 8 - 9: Lomamyia squamosa CARP., 8: genital sclerites, lateral; 9: paramere-mediuncus-complex, ventral. 10: Naizema mendozina (ESB. - PET.), genital sclerites, lateral. 11: Trichoma graciliperine TILL., genital segments, dorsocaudal. - Fig. 8 - 10 from MacLEOD & ADAMS, 1967; Fig. 11 from U. ASPÖCK & H. ASPÖCK, 1985.

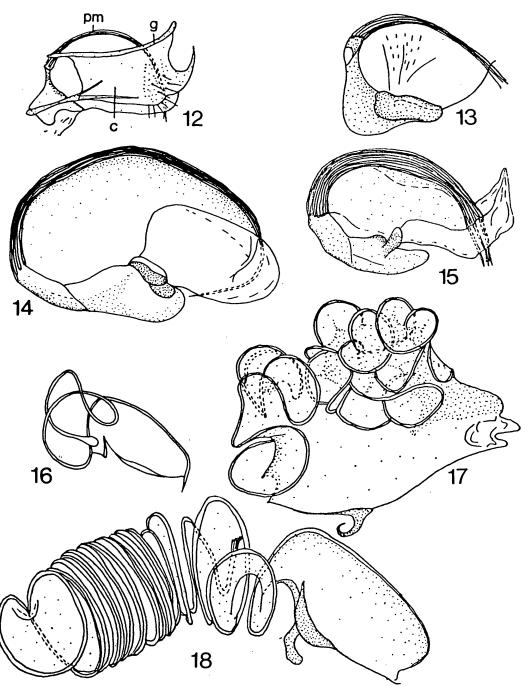


Fig. 12 -18: Examples of the paramere-mediuncus-complex (lateral) of  $\sigma$  genitalia of different berothid genera. - 12: Berotha insolita WALK. 13: Stenobiella cardaleae U. A. & H. A. 14: Asadeteva vartianorum U. A. & H. A. 15: Sphaeroberotha ressli U. A. & H. A. 16: Spermophorella maculatissima TILL. 17: Podallea pellita U. A. & H. A. 18: Isoscelipteron rufum (NAV.). - Fig. 12 from U. ASPÖCK, 1983; Fig. 13 from U. ASPÖCK & H. ASPÖCK, 1983; Fig. 14 and 18 from U. ASPÖCK & H. ASPÖCK, 1981 b; Fig. 15 from U. ASPÖCK & H. ASPÖCK, 1984 a; Fig. 17 from U. ASPÖCK & H. ASPÖCK, 1981 a.

which they spray by waving their abdomen, paralysing and killing termite workers, soldiers and reproductives. Although the encouraging experiences with Lomamyia latipennis CAR-PENTER are not necessarily applicable to other species and should therefore by no means be uncritically generalized, they nevertheless represent a model for the exploration of all other species.

#### **CHOROLOGY**

The Berothidae occur on all continents (Fig. 28) with distribution areas predominantly in warm-temperate, subtropical and tropical zones. Whilst the Berothinae represent the approximate distribution of the family, Nosybinae and Rhachiberothinae are, by contrast, restricted to Africa and the Cyrenoberothinae to South America. Endemic and non-endemic genera counterbalance each other. Australia harbours most endemic genera, that is, five: Stenobiella TILLYARD, Trichoma TILLYARD, Trichoberotha HANDSCHIN, Spermophorella TILLYARD, and Austroberothella U. ASPÖCK & H. ASPÖCK. Africa shelters three:

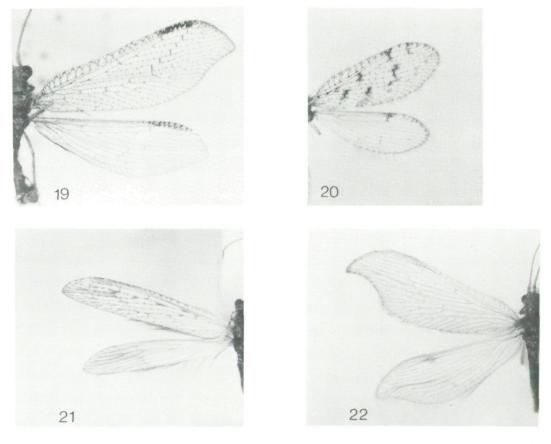


Fig. 19 - 22: Wings of different genera of Berothinae. Identical scale (10 mm = 1,3 mm). - 19: Berotha insulana U. A. & H. A., \$\frac{1}{2}\$. 20: Sphaeroberotha vartianella U. A. & H. A., \$\frac{1}{2}\$. 21: Stenobiella theischingerorum U. A. & H. A., \$\frac{1}{2}\$. 22: Asadeteva vartianorum U. A. & H. A., \$\frac{1}{2}\$.

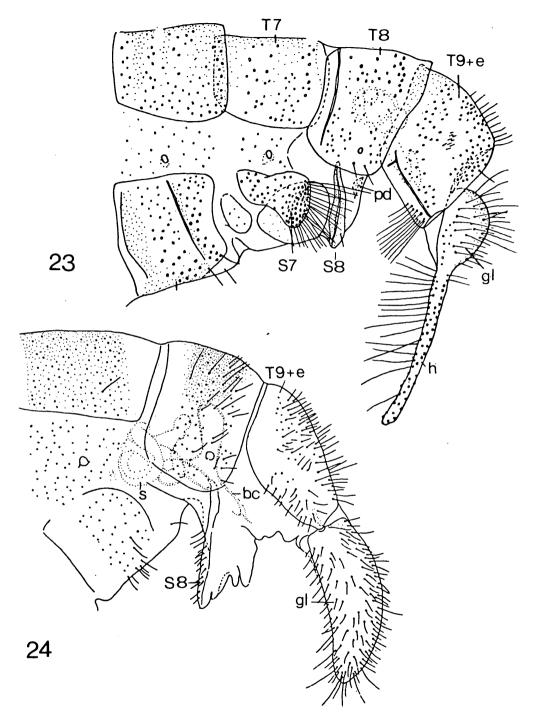


Fig. 23 - 24: Examples of Q genitalia (lateral) of different berothid genera. - 23: **Berotha indica** (BRAU.). 24: **Nosybus zernyi** U. A. & H. A. - Fig. 23 from U. ASPOCK, 1983; Fig. 24 from U. ASPOCK & H. ASPOCK, 1983.

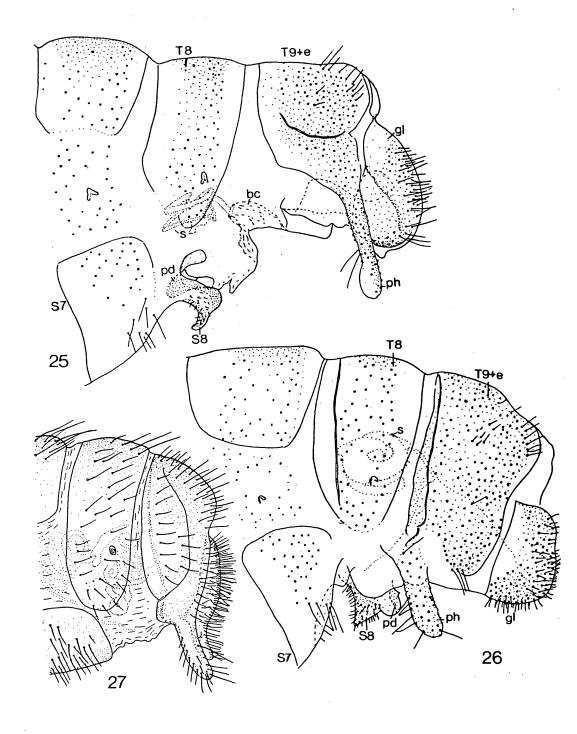


Fig. 25-27: Examples of Q genitalia (lateral) of different berothid genera. - 25: Austroberothella rieki U. A. & H. A. 26: Protobiella zelandica TILL. 27: Mucroberotha fasciata TJED. - Fig. 25 - 26 from U. ASPÖCK & H. ASPÖCK, 1985; Fig. 27 from TJEDER, 1959.

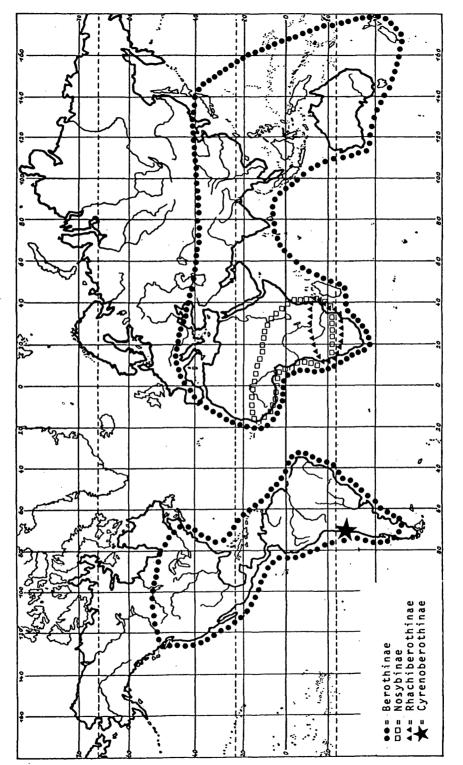


Fig. 28: World distribution of the 4 subfamilies of Berothidae.

Rhachiberotha TJEDER, Mucroberotha TJEDER, and Nosybus NAVAS. South America has two endemic genera: Cyrenoberotha MacLEOD & ADAMS and Naizema NAVAS. Distribution of Lomamyia BANKS extends over both Americas (including Cuba!) (PENNY 1983), and is thus not strictly endemic. Asadeteva U. ASPOCK & H. ASPOCK is known only from Afghanistan and Pakistan, and Protobiella TILLYARD only from New Zealand. Berotha WALKER seems to be restricted to the Oriental region. The genera Sphaeroberotha NAVAS, Podallea NAVAS, and Lekrugeria NAVAS each occur in Africa and Asia. Sphaeroberotha is well represented on both continents, Podallea occurs mainly in Africa and Lekrugeria, with only a few known specimens, has a broad disjunctive distribution between Africa and India. Isoscelipteron COSTA has the widest distribution: southern Europe, northern Africa, Asia, northern Australia, the Nicobars, and Solomon Islands. It is thus not only an extremly evolved genus but also a very successful one!

The distribution of most species is very poorly and unsatisfactorily known and we are still far from understanding the actual zoogeography of Berothidae and factors affecting it.

#### Abbreviations

bc = bursa copulatrix pd = pudiculum .

 $c = 9^{th} coxopodite$  ph = pseudohypocauda

e = ectoproct pm = paramere-mediuncus-complex

g = gonarcus S = sternite

gl = gonapophyses laterales s = spermatheca

h = hypocauda T = tergite hy = hypandrium internum t = torulus

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