Revision of the family Alycidae (Acariformes, Acari), with special reference to European species

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Abstract

This thesis provides a proposal to divide Alycidae G. Canestrini & Fanzago into two subfamilies and four tribes. Three of the tribes (Alycini G. Canestrini & Fanzago new rank; Bimichaeliini Womersley new rank; Petralycini new rank) include European members and are defined here. Also a preliminary generic division for both the Alycini and Bimichaeliini is introduced. This new hierarchy is based on a reassessment and reranking of new and previously known synapomorphies of the clusters concerned by cladistic analysis, using 60 morphological characters for 48 ingroup, one sister group and one outgroup species. Of special importance are the following conclusions: (1) Petralycini differ from two other major lineages by the unique structure of the prodorsum and palpi; (2) Bimichaeliinae share the presence of large lamellae and the same structure of chelicera, but there are distinct groups on the grounds of secondary and primary patterning of the integument which represent different evolutionary trends; (3) Alycini are united by presence of a reduced pair of lateral eyes but there are distinct groups on the grounds of cheliceral structure and the patterning of integument. The fine morphology of integument was revealed by Scanning Electron Microscopy. The basic characters of the taxa are illustrated either by SEM micrographs or by outline drawings. The subfamilies, tribes, genera and all European species known to now are (re)described and keys to all the ranks are given.

The presented classification of Alycini includes the redescriptions of *Alycus* C.L. Koch, *Pachygnathus* Dugès and *Amphialycus* Zachvatkin. *Orthacarus* Zachvatkin is reduced to a new subgenus of *Amphialycus* (new rank). The species described or redescribed are: *Pachygnathus wasastjernae* sp. nov. from Finland; *Pachygnathus villosus* Dugès [in Oken] (as a senior synonym of *P. ornithorhynchus* Grandjean); *Alycus roseus* C.L. Koch; *Alycus denasutus* (Grandjean) comb. and stat. nov.; *Alycus trichotus* (Grandjean) comb. nov.; *Alycus marinus* (Schuster) comb. nov.; *Amphialycus* (Amphialycus) *pentophthalmus* Zachvatkin; *Amphialycus* (Amphialycus) *leucogaster* (Grandjean); and *Amphialycus* (Orthacarus) *oblongus* (Halbert) comb. nov. *Alycus rostratus* Trägårdh is synonymized with *A. roseus*; *Pachygnathus berlesei* Bottazzi and *P. lombardinii* Bottazzi are synonymized with *A. trichotus*; *Pachygnathus arhinosus* Willmann is synonymized with *A. leucogaster*; and *Orthacarus tremli* Zachvatkin is synonymized with *A. oblongus*.

The European members of the worldwide *Bimichaelia* Thor are divided into two genera: *Bimichaelia* s.s.t. Thor and *Laminamichaelia* new genus. *Bimichaelia crassipalpis* Halbert, *B. campylognatha* Grandjean and *B. rectangula* Willmann are synonymized with *Bimichaelia sarekensis* Trägårdh; *Michaelia clavigera nomen nudum* in Castagnoli & Pegazzano, *Bimichaelia diadema* Grandjean and *B. praeincisa* Willmann are synonymized with *Laminamichaelia setigera* (Berlesei) comb. nov.; *Bimichaelia stellaris* Womersley and *B. ramosa* Mihelčič are synonymized with *Laminamichaelia arbusculosa*
(Grandjean) comb. nov. *Bimichaelia augustana* (Berlese) and *Laminamichaelia subnuda* (Berlese) comb. nov. are redescribed. Descriptions of Petralycini and *Petralycus unicornis* Grandjean are rewritten in accordance with the other diagnoses given here.

The Devonian genus *Protacarus* Hirst was found to share none of the derived character states used in the modern delineation of Alycidae. *Coccalicus clavatus* Willmann belongs to a tydeoid cluster. *Rhyncholophus devius* C.L. Koch and *Pachygnathus cavernicola* Oudemans are considered as species inquirendae.

The following points are discussed: (1) reasons for the model of description, division into subfamilies and tribes and prodorsal evolution are given; (2) the importance of the sensory organs in defining the species and non-linearity in evolution of the reductive trends of chelicera and palpi between the proposed subfamilies and tribes emphasized; (3) positions of these primitive mites and other major lineages in existing cladograms; and (4) some pros and cons in working with SEM.

A database of prodorsa, illustrated in details using SEM, might be an answer to future needs of species identification in soil zoology, ecology and conservation, as proposed in Appendix 2.

Selected figures of an undescribed bimichaeliine species ‘sil’ from South Africa, which forms a monotypic sister-group to all the rest of the Bimichaeliinae in the analysis, are given in Appendix 3.

**Key words:** Acari, Endoestigmata, Alycidae, cladistics, classification, new taxa, Bimichaeliinae, Bimichaeliini new rank, Alycinae, Alycini new rank, Petralycini new rank, Europe
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1. Introduction

Family Alycidae includes some of the most primitive extant mites on earth. They are soft-bodied segmented predators or sap-suckers, 300-2000 μm in length, thelytokous and ubiquitous in terrestrial ecosystems. Soil surface habitats, such as rotten wood, moss, litter, humus but also the soil proper are repeatedly listed for the members of Alycidae. The free-living species very likely move about between the aforementioned biotopes and the most favoured microhabitat of individual species still usually remains uncertain. The family is worldwide in distribution. However, the verified records so far are scanty and the sampling localities too sparsely situated on the globe for any detailed distribution map of any of the species.

Alycidae form part of the superorder Acariformes (Actinotrichida) which has been divided into two orders, Trombidiformes (incl. Prostigmata and some families of Endeostigmata) and Sarcoptiformes (incl. Oribatida [= Cryptostigmata], Astigmata and most of the endeostigmatic families). The Alycidae are either accepted as a basal group of Sarcoptiformes (Norton et al., 1993) in the superorder Acariformes (Proctor, 1998), or more prudently, assigned, together with several endeostigmatic families, Trombidiformes and Sarcoptiformes to the superorder Prostigmata (Walter et al., 1996), which is treated as order in the Fauna Europaea listing (Judson & Uusitalo, 2005).

The intense early descriptive work on European taxa of Alycidae (and Prostigmata and Endeostigmata in general) was based on characters observed with bare eye from intact specimens (colour, shape) or with light microscope with low magnification (e.g. Dugès, 1834; C.L. Koch, 1841 – 1844; Berlese, 1884, 1904, 1910). The inadequacies of these descriptions, which often concentrated on superficial characters, often mislead later students in the field (e.g. Trägårdh, 1910; Halbert, 1920, 1923; Womersley, 1944; Bottazzi, 1950a, b; Mihelčič, 1956; Willmann, 1956) into establishing new species or synonymies on inadequate grounds. Inevitably, this is also reflected in modern research. E.g. Kethley (1990a) summarized species compositions of the major mite groups in the decomposer food webs of the world’s major land ecosystems and according to him Prostigmata (incl. Endeostigmata and Alycidae) compete with the oribatids in abundance but data on the Prostigmata communities in temperate coniferous forest, which covers large parts of Europe (and Asia and North America), was missing because the taxonomy was inadequate to allow species identification (Dr. Kethley, pers. comm., see also Coleman & Crossley, Jr., 2003).

In my attempt to work at the species-level with soil Prostigmata (Actinedida) and Endeostigmata in the boreal coniferous forest biome, more than fifty taxa were discovered. Among them were two species, representing the old genera *Alycus/Pachygnathus* and *Bimichaelia* of the family Alycidae, which were found in litter and soil of a Scots pine (*Pinus silvestris*) forest stand in Finland (Uusitalo, 1993; Uusitalo & Huhta, 1995). Most of the identification work was never completed. Not only the poor quality of the early European descriptions but also the so many unequal illustrations of the global fauna effectively prevented reliable identification of the species. It seemed obvious that a resolution of the taxonomic questions was required before any serious survey of other aspects of soil zoology of these mites could be performed.

Accordingly, the aim of this paper is to initiate revisionary work on the European nominal species of the Endeostigmata in the family Alycidae G. Canestrini & Fanzago, 1877. Kethley (1982) stated that the family contains 7 nominal genera and 34 nominal species, but only 4 of the genera and 11 of the species were recognizable. Alycidae formed part of an assemblage of primitive mites called Endeostigmata, which
included 159 free-living species in 28 genera and 11 families (Norton et al., 1993). This group is now known to be paraphyletic: two of the families (Lordalycidae and Sphaerolichidae) are close outgroups of Prostigmata within Trombidiformes (see also Chapter 9.2.6.), while the others constitute the basalmost group in the lineage Sarcoptiformes, leading to oribatid and astigmatic mites. The family seemed ideal to start with, because of the substantial collections of fresh material at ZMT, collected world-wide, and because of the fundamental papers of the French fauna by Grandjean (1936, 1937a, 1937b, 1937c, 1937d, 1942, 1943), were available for comparison.

1.1. Alycidae G. Canestrini & Fanzago

1.1.1. Synonymy

Synonymy lists of the mites revised here have also been published by Oudemans (1937) and Thor & Willmann (1941). Jacot (1932) remarked that one thing appreciated by acarologists in Oudemans' History of Acarology ("Kritisch Historisch Overzicht der Acarologie") is the creation of a broad working basis by bringing together all early references on the group. However, most of the entries in the synonymy lists given by Oudemans (1937: 865-869) for Pachygnathus/Alycus, Alycus devius and Pachygnathus villosus has been criticized for good reason. As Jacot (1932) noted, most of the Oudemans' references refer to relisting in compilations and translations, or later editions or reprints, and are therefore of no systematic or biological interest, and he firmly criticized the way Oudemans made synonymies without offering any evidence (see also Michael, 1902). Similar deficiencies are also present in the synonymy lists given by Thor and Willmann (1941) and me. In the context of this first revision of Alycidae it seemed desirable to relist the published entries once more, together with some more present ones, which may be of common interest.

From 1834 to 1877 the oldest genera Pachygnathus Dugès, 1834 and Alycus C.L. Koch, 1842 most often were included in Trombidiidae Leach, 1814 (Trombidiei in Dugès, 1834a). G. Canestrini & Fanzago (1877) transferred Alychus (sic!) into a monotypic family Alychini, which Berlese (1885) adopted as a subfamily, Alychidae, for both Alychus, which he synonymized with ?Pachygnathus, and Michaelia Berlese, 1884 (=Bimichaelia Thor, 1902). Since then, the genera have been considered as a group, but the name has varied according to whether the names Pachygnathus, Alycus or Bimichaelia where considered valid. The issue had been debated for over a century till Judson (2000) solved the problem in favour of Alycidae. For more details, see synonymy under Alycidae.

Alycini was identical to the Alycidae of this work during a short period in the late 1800's when most of the endeostigmatids of today were still undiscovered and undescribed. Since then, the composition of Alycidae has varied a lot, depending on the period and author, due to the vague delineation of the family. Because of this, the family names Alycidae or Pachygnathidae or Bimichaeliidae of the late authors have very little to do with the subfamilies or major lineages (the tribes) proposed here although they share the same name.

As a rule, in the synonymy below the authors have listed genera and/or species which belong to the tribes of this work (Alycini, Bimichaeliini and Petralycini, see Chapters 4, 5 and 6) but the family name was understood by authors also to cover a wide variety of genera and species, now in other families, see below in Section 1.1.3., and
Remarks (2). For brevity, a comment “(in part, Pachygnathus/Alycus and/or Bimichaelia and/or Petralycus only)” is omitted, but in practice, it should be added after most of the entries. The relevant generic names and species mentioned in the papers can be found in synonymies farther behind. Only a family-group record is given e.g. by Price (1973); André (1979); Hoy & Shea (1981); Vázquez & López-Campos (1996), see also Chapter 9.1.

Family Alycidae G. Canestrini & Fanzago, 1877

Alychinii G. Canestrini & Fanzago, 1877: 168, misspelling for Alycini, based on Alycus.

Alycidae Berlese, 1885: 134, erroneous orthography; Berlese, 1887, A.M.S. fasc. 45 no 5; G. Canestrini, 1891: 18; 1889a, A. M. S. fasc. 57 no. 10; Ewing, 1913: 123 (not G. Canestrini & Fanzago, 1877); Womersley, 1937: 6 (not G. Canestrini & Fanzago, 1877).

Alichidae Berlese, 1893: 31, erroneous orthography; Berlese, 1899b: 317, key to families; Berlese, 1913b: 4; Halbert, 1920: 12 (not G. Canestrini & Fanzago, 1877).


Alichininae Trouessart, 1914: 13, misspelling.


Pachygnathinae Oudemans, 1929: 426 (not G. Canestrini & Fanzago, 1877), misspelling.

Pachygnathiidae Oudemans, 1903a: 58, key, misspelling; Oudemans, 1904: 98, key to subfamilies; Oudemans, 1905: 241.


Pachygnathiidae Vitzthum, 1929: 46, key, unjustified emendation.

Pachygnathiidae Evans, 1953: 806, unjustified emendation.

Bimichaeliae Womersley, 1944: 134, based on Bimichaemia, misspelling.


1.1.2. Characterization of Alycidae

Body and skin (Fig. 26): Length 200-2000 μm; body sack-like; opisthosoma soft; epicuticular integument hard on chelicerae, prodorsum, subcapitulum, genital valves and legs; surface of hard integument ornamented by small granules or by parallel striae of various length on friction surfaces, e.g. adaxial sides of femora and trochanters (Fig. 118) and abaxial sides of chelicera (Fig. 74); procuticular network under the surface structures;
dorsal setae ciliated, simple; ventral setae smaller, less ciliated; additional setae commonly: on ventral side in most stages, dorsally and in appendages in most cases; sejugal furrow well developed (Figs. 36, 120); opisthosomal segmentation evident at least in larval stage.

Prodorsum (Fig. 8): naso present in most cases; two pairs of bothridial sensilla (ve and sci); anterior pair of sensilla (ve) inserted on proper prodorsum (i.e. not on naso, not set in a communal depression); peritremes absent.

Gnathosoma (Fig. 29): labrum unsclerotized, labium small, lateral lips with or without adoral setae, chelicerae chelate-dentate, fixed cheliceral digit normally produced (=not truncate), cheliceral bases free; subcapitulum anarthric.

Palps (Fig. 50): linear (i.e. without a clawlike seta); five segments; one solenidion on tarsus; eupathids (ξ) apically on tarsus.

Genital and anal areas (Fig. 7): genital opening a longitudinal slit, well removed anteriorly from anal opening; a row of setae on genital valve usually closer to mesal margin, additional setae randomly distributed; aggenital setae flanking the valves; 3 pairs of discoid genital papillae; eugenital setae in the progenital chamber also in tritonymphal stage; anal opening ventral in most cases.

Legs (Fig. 91): four pairs of walking legs; coxisternal plates I and II contiguous, separated from each other; empodia with setules, symmetrically paired claws with fine ribbing; lyrifissures proximally on palpal and pedal tarsi (Fig. 80); famulus (ε) present on tarsi I (Fig. 99); leg setae finely ciliated; pseudacanthoid eupathids ventro-distally at least on pedal tarsi I; leg trichobothria absent; solenidia at least on tarsi I, II (ω), tibiae I-III (φ), genua I-IV (α), femur I (θ); solenidia short. Adults free-living; larva homomorphic; protective scale of larval organ present.

1.1.3. Historical background of Alycidae

To get a clear picture of how the currently accepted composition of the family Alycidae was determined, the steps taken by Grandjean must be considered in more detail. The family name Alycidae was most inclusive when Grandjean (1937d: 265) proposed the name *Endeostigmata* for this group of prostigmatid mites which did not have prostigmata or tracheal openings at the base of chelicera. The taxon then included the genera *Bimichaelia* Thor, 1902, *Hybalicus* Berlese, 1913, *Nanorchestes* Topsent & Trouessart, 1890, *Pachygnathus* Dugès, 1834, *Speleorchestes* Trägårdh, 1909, *Sphaerolichus* Berlese, 1904, *Sebaia* Oudemans, 1903 and *Willania* Oudemans, 1931 (= *Épistomalychus* Thor, 1931). Grandjean noted that these genera were "réunit quelquefois sous le nom de Pachygnathidae ou Alycidae mais il est clair qu'ils représentent un groupe très diversifié, beaucoup plus étendu qu'une famille", while he proposed family *Nanorchestidae* (p. 268) for *Speleorchestes* and *Nanorchestes*. (As explained by Judson (1995), the family Nanorchestidae should in fact be attributed to Berlese (1913b), who proposed the tribe Nanorchestini). Later, Grandjean (1939: 4) again expanded the concept of "Endeostigmata" and established new families not only for older genera but also for several new generic names: Lordalycedae for *Hybalicus* and *Lordalycus* Grandjean, 1939; Sphaerolichidae for *Sphaerolichus*; Alicorhagiidae for *Alicorhagia* Berlese, 1910 (= *Willania*); Terpnacaridae for *Sebaia*, *Terpnacarus* Grandjean, 1939 and *Alycosmesis* Grandjean, 1939. He also transferred *Caenonychus* Oudemans, 1902 to Nanorchestidae. The remaining genera, *Pachygnathus* (=*Alycus*) and *Bimichaelia*, were left in the Pachygnathidae Kramer, 1877 (=Alycidae). Later genera described in Alycidae were
Petralycus Grandjean, 1943, from France, Amphialycus Zachvatkin, 1949 and Orthacarus Zachvatkin, 1949 from the Ukraine, and Coccalicus Willmann, 1952 from the Netherlands. The extinct Devonian genus Protacarus Hirst, 1923 from Scotland, was transferred to the family by Thor & Willmann (1941).

Most of the character states listed above (Section 1.1.2.) as well as those used by earlier authors (see Appendix 1) are considered plesiomorphic (ancestral), based on outgroup comparison with other endostigmatic families or non-mite arachnid taxa (e.g. Lindquist, 1984; O'Connor, 1984; Kethley, 1990a; Lindquist & Palacios-Vargas, 1991; Evans, 1992). The evolved character states are the common presence of additional setae and adding of eugenital setae in the progenital chamber also in the last nymphal stage. In other words, lumping of the historical (traditional) three genera (Alycus, Bimichaelia and Petralycus) into one family might be based on plesiomorphic similarity (Lindquist & Palacios-Vargas, 1991: 360) and thus the family Alycidae (=Bimichaeliidae sensu Kethley, 1982) could be considered as a paraphyletic group instead (for a detailed historical, see Section 1.1.4.), if those two character states were convergently evolved, i.e. separately in different genera.

1.1.4. Searching for monophyly of Alycidae in the past

Early characterizations of Alycidae were based on evolutionary systematics, meaning that its members were grouped on the basis of overall similarity, rather than on synapomorphies. For example, Grandjean (1943) included the genus Petralycus in the family because of the character states shared with his concept of Pachygnathus (i.e. Alycini of this thesis), namely the pattern of prodorsal apodemes, form of rutella (his maxillae), and divided fourth femora. The apodemes serve as an attachment for muscles that control movements of the chelicera. The robust chelate-dentate basic pattern of the chelicerae of both genera is considered plesiomorphic, from which it can be inferred that the pattern of apodemes is also primitive. The lobed membrane of rutella and divided femora are also considered primitive by authors.

The possibility that the family would eventually have to be split up was envisaged by Grandjean (1943: 19) who wrote: "La famille des Pachygnathidae a besoin, pour contenir les 3 genres, d’être entendue dans un sens très large, mais le moment n’est pas venu de la diviser".

Womersley (1944: 134) proposed a ‘new’ family for nanorchestids and divided rest of the Alycidae into two subfamilies, Alycinae and Bimichaeliinae, on grounds of cheliceral structure, without being aware of Petralycus Grandjean, 1943 and Nanorchestidae Grandjean, 1937 (for correct attribution to Berlese, see Section 1.1.3). None of the eight characters used by Womersley to define Alycidae can be considered synapomorphic for the group, which still included genera like Sphaerolichus, Hybalicus, Leptalicus and Paralycus.

Lindquist & Palacio-Vargas (1991: 360) challenged the monophyly of Bimichaeliidae (=Alycidae) stating that the only derived character state (neotrichy) does not hold well for some members (Petralycus) of the family. Arguments were proposed by them for two clusters: one including Alycus, Amphialycus, Pachygnathus, and the other including Bimichaelia and Petralycus. For the first cluster they did not specify any common character state, but briefly mentioned plesiomorphic states. For the Bimichaelia/Petralycus cluster they propose several synapomorphies: (1) attenuated or pointed lateral lips on subcapitulum; (2) reduced rutella; (3) loss of adoral setae; (4)
reduced number of palpatarsal eupathidia; (5) loss of lateral eyes; (6) one of the two pairs of prodorsal trichobothria clavate or capitate; (7) padlike empodium on all leg tarsi. In addition to (1), (5) and (7) Grandjean (1943: 2) also listed: (8) non-lobed labrum; (9) four eugenitals; (10) loss of famulus II; (11) loss of iteral setae except perhaps on leg I. Most of these apomorphies (2, 3, 4, 5, 7, 10, 11) are based on regressive evolution (see Chapter 9 and Chapter 3.1, Lineage VI for character 7). The loss patterns are similar in both lineages and a common origin in the cases of complete loss is hard to prove, if the material is small, based mainly on literature or without a proper cladistic analysis, and the character states might be due to convergence. Lindquist & Palacio-Vargas (1991) did not publish a list of the characters included in their analysis; evolution of some characters (1, 8) is linked with the gnathosomal structures, which have evolved separately due to different feeding strategies; one character (6, i.e. globularity of setae ve versus sci) does not involve homologous organs; and one character state (9) does not hold well for all the members concerned and is probably plesiomorphic.

There are a few shared derived states, however, as presently proposed for the family Alycidae: presence of additional setae or neotrichy (O’Connor 1984) and the presence of eugenital setae in nymphal stages (Kethley 1991).

When the whole dorsum is neotrichous, the middle setae are longest on caudal segments of the Alycini and equal in size in the Bimichaeliini, whereas in Petralycini the caudal segments are holotrichous and the setae are inserted in rows (cf. e.g. Figs. 72 vs. 131 vs. 141, respectively). The larvae of Alycus roseus (Fig. 152), Bimichaelia campylognatha (Grandjean, 1943: 48) and Petralycus unicorns (Grandjean, 1943: 10) are holotrichous. Theron (1977) has described species of Petralycus with opisthosomal neotrichy from South Africa, but the dorsal idiosoma of the most primitive Petralycus species is holotrichous in the adult stage. A dorsally holotrichous alycid from Oregon, identified as Pachygnathus, has been illustrated by Krantz (1978: 312, Figs. 57-1, 57-3). The differences in the neotrichy patterns of the major lineages defined in this work also suggest a parallel evolution. In addition, groups such as velvet mites, water mites, Strandmanniidae and Labidostommatidae have additional setae on the dorsal and ventral sides of the body. These observations provide additional support for the idea that neotrichy has arisen several times in Alycidae (see character 10 in section 2.4 for coding used in this study.

Juvenile eugenitals can also be interpreted as a character release due to neotrichy during ontogeny (Kethley, 1991). Kethley proposed examination of other neotrichous taxa (e.g. Speleorchestes: Nanorchestidae) to test if the presence of eugenitals in juveniles has become developmentally linked with neotrichy. Kethley (1982: 118) stated that hypertrichy (=strong neotrichy) had evolved independently in Bimichaeliidae (=Alycidae) and Nanorchestidae.

A possible neotrichy of the eugenital setae could also be assessed by other means. Unlike the fundamental setae, neotrichous setae are often smaller in size, the number of additional setae may vary in a specific way, and the number may differ on the left and right sides of an individual. Grandjean (1943: on pages 8; 42; 47; 50; 57, respectively) reports that the number of eugenital setae in males of Petralycus varies between 9 and 10; the number of small eugenital setae on tritonymphs of Bimichaelia arbusculosa is usually 4 but often there is none; the solitary male of Bimichaelia campylognatha had 7 or 8 eugenital setae on each side of the penis and tritonymphs had either one or two pairs; tritonymphs of Bimichaelia diadema usually had 2, sometimes only 1 eugenital seta.
All kinds of organs and areas on neotrichous species show additional setae and there is no reason to expect the progenital chamber of juveniles to be an exception - a neotrichy-proof area. There seems to be no reasonable function either, for the setae in a progenital chamber without genitalia, unless they have a role in the function of genital papillae. Additional setae can also be found on genital and aggenital areas of all the members involved but this is not unique to the Alycidae. These observations seemed to support the possibility of an ontogenetic character release of a state previously restricted to the adult stage and, consequently, the number of eugenital setae in adults and juveniles could both be considered as a manifestation of neotrichy.

In conclusion, a hypothesis of homoplasy is plausible for neotrichy and for juvenile eugenitals and, consequently, the Alycidae might be rejected as a natural group. In other words all the advanced character states thought to be shared by the members of Alycidae could be explained instead as a result of independent evolution.

At this point, a new phylogenetic analysis therefore seemed necessary. Relationships within the family are studied here using cladistic methods. This does not address the wider question of the monophyly of Alycidae, which is outside the scope of this thesis.

2. Material and methods

2.1. The specimens

The old European material for this study originates from: the Berlese Collection, the Halbert Collection; the Mihelčič Collection; the Trägårdf Collection; and the Willmann Collection, as indicated below. Also available from Europe were the recent collections in alcohol at ZMT, numerous slides from ISZA, Italy and my own collections mainly from the Nordic countries, Ireland and the Mediterranean region. The world fauna available for comparisons originated from Polynesia, in the Lehtinen Collection at ZMT; from North America, in the OSU Collection; from South Africa, in the Theron Collection at PU; from Australia, in the Womersley Collection at SAM; and from Siberia, in my own collection. The samples taken by myself were extracted on the spot using a collapsible, full-sized Berlese-funnel system (Norton & Kethley, 1988).

Abbreviations for museums and institutions:
BA = Berlese Acaroteca, Cascine del Riccio, Firenze, Italy
ISZA = Istituto Sperimentale per la Zoologia Agraria, Cascine del Riccio, Firenze, Italy
MNCN = Museo Nacional de Ciencias Naturales, Madrid, Spain
NMB = Naturhistorisches Museum, Basel, Switzerland
NMI = National Museum of Ireland, Dublin, Ireland
NRM = Naturhistoriska Riksmuseet, Stockholm, Sweden
OSU = Ohio State University, Columbus, OH, USA
PU = Potchefstroom University for CHE, Potchefstroom, South Africa
SAM = South Australian Museum, Adelaide, Australia
SMF = Senckenbergmuseum in Frankfurt, Germany
ZMT = Zoological Museum, University of Turku, Finland
ZSS = Zoologische Staatssammlung, München, Germany
Abbreviations for collectors:
AB = Antonio Berlese
AT = A. Thienemann
CW = Carl Willmann
FG = F. Grandjean
GK = Günther Krisper
HG = Helena Granlund
HC = H.M. Cooper
IT = Ivar Trägårdh
JH = J.N. Halbert
JS = Josef Schweizer
MS = M. Sellnick
MU = Matti Uusitalo
OL = O.V. Lindqvist
PT = Pieter Theron
PL = Pekka T. Lehtinen
RN = Roberto Nannelli
RS = Reinhard Schuster
VH = Veikko Huhta
WS = W. Steiner

The specimens under **Unchecked published records** (Unchecked in the lists for brevity) have not been actively traced. Rechecking of all the European records under *Bimichaelia sensu lato, Alycus* and *Pachygnathus* is beyond the scope of this paper, but it should be done to confirm their current status in the new classification.

According to Bottazzi (1950a: 32) the slides labelled as *A. roseus* at BA are in poor condition. Whether they are recognizable to species any more, remains unknown at the moment. The specimens labelled *Pachygnathus roseus* and *P. lombardinii* (Bottazzi, 1950b) are probably deposited at the Zoological Institute in the University of Parma, where Bottazzi used to work, but the attempts to locate the slides have not been successful so far.

Frenzel's Collection was destroyed during World War II (bombed) according to Dr. Sellnick (Prof. R. Schuster in litt.).

Prof. Travé kindly sent me two specimens of *Petralycus unicornis* in alcohol and a specimen of *Pachygnathus dugesi*, in lactic acid, all identified by Grandjean. Unfortunately, the tubes were crushed in the mail. Two of the specimens had vanished and the one remaining *Petralycus* had deteriorated in the lactic acid and proved to be useless as a SEM-specimen. Most probably there are more specimens of the syntype series of *Pachygnathus dugesi* (and *P. d. denasutus, P. trichotus, P. ornithorhynchus, P. leucogaster*), as well as specimens of the syntype series of *Petralycus unicornis* (and *Bimichaelia arbusculosa, B. campylognatha and B. diadema* and French specimens of *B. subnuda*, Berlese) in the Grandjean's Collection, but his minutely detailed descriptions and illustrations are exceptionally good substitutes for light microscopy. Grandjean was opposed to the idea of type designation because of the need for dissection in descriptive work (Grandjean, 1967: 255, and Dr. Travé, in litt.).

The slides of the Halbert Collection at NMI are in poor condition and because of their fragility; the museum is not willing to send them on loan (Dr. James P. O'Connor, pers. comm.). Only Halbert’s putative types from Ireland are listed in the catalogue of the collection in Dublin (O’Connor, 1980). Thus, for example, *Alycus oblongus* Halbert is listed and *Bimichaelia crassipalpis* Halbert is known to be lost,
whereas *Alicus rostratus* Trägårdh is absent from the list, even though it is present in the Collection (see also Luxton, 1998 and Baker & Bayliss, 2005).

The collection of *Alycus roseus sensu* L. van der Hammen at the Rijksmuseum voor Natuurlijke Historie in Leiden, The Netherlands was not available for me, but van der Hammen (1969) found his material of *Alycus roseus* from Arnheim to be identical with topotypic specimens of *Pachygnathus dugesi* from Mongaillard, France where I have successfully collected material.

Thor's Collection was destroyed in accordance with his will (Zacharda, 1980: 666, Marshall et al., 1987: 4).

The records of *Bimichaelia setigera* from Japan and *B. arbusculosa* from Malaysia by Shiba (1968 and 1976, respectively) have not been verified.

Trägårdh's collection, NRM in Stockholm is in a miserable state. He did not take proper care of slides and wet material. Later on, some assistant remounted a part of the slides but left the labels loose, causing a mixture of slides and information. The original holotype of *Bimichaelia setigera var. sarekensis* is at least temporarily lost (Curator T. Kronestedt, in litt.).

The two specimens identified as *Alycus ? roseus* are lost from the Womersley Collection, SAM (Dr. David Hirst, in litt.).

The original specimens of *Amphialycus pentophthalmus* and *Orthacarus tremli* are not preserved. There is no Zachvatkin Collection at the Moscow Zoological Museum where he used to work. Dr. Zachvatkin was of the opinion that his descriptions were accurate enough to recognize the species (Dr. K.G. Mikhailov, pers. comm.).

In the rest of the text, this Chapter 2 is refered to as Material only.

The old types and other slide material were examined mainly by phase-contrast microscopy and, in the case of fresh material, by SEM (Scanning Electron Microscope, JEOL JSM-5200) after dehydration by CPD (critical point drying) and coating with gold. The specimens were mounted in lateral position on stubs using micro-needles (Norton & Sanders, 1985) to enable the observation of both dorsal and ventral surfaces.

In the chapter headed Records, the letter U plus a number (e.g. U123) refers to the access number of the stub on which a specimen has been SEM-mounted and which is deposited at ZMT. The letters LH mean litter and humus in sampling data.

The synonymy lists include all the entries listed earlier and so several entries refer to papers in which the scientific name has been mentioned only in connection to other species when morphology, habits, etc. have been compared (for history, see Chapter 3.1.). Closely related comments have been connected by numbered Remarks throughout the paper in order to facilitate finding the relevant notes.

### 2.2. Phylogenetic analysis

The data matrix for analysis (Table 1) was constructed and manipulated with the computer program WinClada, version 1.00.08 (Nixon, 2002). Phylogenetic relationships were studied by parsimony analysis using the computer program NONA, version 2.0 (Goloboff, 1999), used together with WinClada, to search for most parsimonous cladograms. The search parameters used with NONA were 'hold100000, hold/100, mult*50 and max*'. The maximum number of trees taken in the memory of the program is 100000. The number of trees simultaneously open during computer run is 100. The order of taxa in the run is randomized, and a tree prepared and swapped 50 times by
connecting branches in various points of the tree. With these parameters, the program makes a heuristic search and swaps branches with ‘tree bisection-reconnection’ (TBR). Unsupported nodes were collapsed to accept only unambiguous support for the nodes in the strictest sense, i.e. only if all possible states between the ancestor and descendant node are different. The resulting cladograms and character optimizations were studied with WinClada. For the analysis, sixty morphological characters were coded for 48 ingroup and two outgroup taxa. The characters were equally weighted in the analysis. Multistate characters were treated as unordered: this is the most neutral way to avoid unwarranted assumptions when evolutionary directions are unclear or unknown.

2.3. Species included

Selected species were used as terminals. After critical examination of the twenty-six European nominal taxa of the Alycus/Pachygnathus–complex, the Amphialycus/Orthacarus–complex, Bimichaelia and Petralycus, the following fifteen species were accepted for the ingroup. Arguments are given further on in the chapters of the tribe. The new synonymies, ranks and combinations for species and genera have already been taken into account in the online list of Fauna Europaea (Judson & Uusitalo, 2005), but not the new taxa.

arbusculosa Grandjean, 1943
gustana Berlese, 1884
denasutus Grandjean, 1937
leucogaster Grandjean, 1937
marinus Schuster, 1958
oblongus Halbert, 1920
pentophthalmus Zachvatkin, 1949
roseus C.L. Koch, 1842
sarekensis Trägårdh, 1910
setigera Berlese, 1904
subnuda Berlese, 1910
trichotus Grandjean, 1937
unicornis Grandjean, 1943
villosus Dugès [in Oken], 1836
wasastjernae sp. nov.

The following thirteen species assigned to Alycidae by previous authors also were included on grounds of the old slide material and literature available. The terminals are listed in the matrix by full name but coded by three initials of their species name only in the phylogenetic tree to allow direct recognition of the European fauna in the topology.

australis Womersley, 1944
brevicornis Theron, 1977
caryapecaus McDaniel & Bolen, 1983
celtisacinus McDaniel & Bolen, 1983
dimixsetosa McDaniel, 1980
disetosa McDaniel, 1980
longicornis Theron, 1977
The cosmopolitan species *Anystis baccarum* (Linnaeus, 1758), as described by Smith Meyer & Ueckermann (1987) was selected as the outgroup. It represents the Trombidiformes, the other main branch of Acariformes (Alycidae is traditionally associated with the main branch Sarcoptiformes). The species is far enough from the ingroup and certainly not a part of it, which is essential. An endeostigmatic mite, *Terpnacarus bouvieri* Grandjean, 1939, was also used as a potentially closer outgroup in the analysis. According to Nixon & Carpentier (1993) an outgroup needs not to be a sister group, or more “primitive”, in respect to the ingroup.

### 2.4. Characters used

An attempt was made to prepare a standardized description and focus on sensory organs, other than mechanoreceptors or setae. Setal counts of the organs suspected to be affected by neotrichy, i.e. additional setae (palpi, legs, prodorsum, dorsum and venter), as well as dimensions of organs, which are of questionable value, are neglected in the definitions and analysis. Values given for variable characters, like ‘total length of adult’ or setal numbers on genital and anal valves and prodorsal in-area, must be considered as indicative only. The following precept was adapted for recognizing species: there must be observable differences between the sensory organs, if specimens are accepted as different morphospecies. Focusing on prodorsal sensory area proved to be a most fruitful choice and pedal solenidia and palpal eupathids usually gave support of high value in analyses.

In solenidial formulae, a hyphen (−) is used to separate solenidial numbers of tarsi, tibiae, genua, and femora I, II, III, and IV, respectively. A backslash (\) separates the numbers of solenidia when observed to vary on a segment. In connection with the Bimichaeliini only, the baculiform solenidia (almost the same diameter throughout) are marked by a number before the letter B and the ceratiform solenidia (tapering towards the
tip but still visibly rounded) by a number before C. Solenidia of the sole European member of the Petralycini are all swollen in the middle, or club-like (claviform). Thus the word does not refer to any clavate form in this connection. In the Alycini the number and presence of baculiform solenidia per segment remains unchanged (one per tarsus I, tarsus II, tibia I, tibia II, tibia III and genu II), the rest of the solenidia having more or less tapering appearance (ceratiform or piliform: elongate, with a fine tip, respectively), and form of the solenidia is not indicated by a letter in the solenidial formulae. The names for the solenidial types are adopted from Grandjean (1935). The genus- and family-level character states are illustrated only once, in a representative species, which causes differences in figure sets of the species.

The genera are considerably reorganized. Some characters used up to now in the identification work of species, such as pattern of large lamellae (primary pattern) and baculiform solenidia, as well as new characters like secondary pattern (the pattern in between large lamellae), delineate larger entities, such as species-groups or new genera. The species can be characterized by using form, number and position of ceratiform/piliform solenidia and the form of setae and sensilla. For a complete listing of the characters used in the analysis, see the coding list of character states in Table 2.

A question mark (?) is used to score the unknown and inapplicable states in the matrix. The logic to start numbering of the characters at 0 is that the sets of ten characters will be 0-9, 10-19, 20-29, etc.
Table 1. Data matrix for phylogenetic analysis.

| AFRICA          | OUTGROUP      | Anystis         | Terpnacar us     | Europe         | roseus         | denasatus       | trichotus      | marin us        | villosus       | wasastjernae   | pentophthalmus | leucogaster     | oblongus       | angustana      | saraekensis    | subnada        | arbuculosus    | setigera       | unicornis     | AMERICA       | longicornis    | brevicornis    | carypecaus     | AUSTRALIA      | australica     | novozelandica  | reticulate     | pasilla       | POLYNESIA      | ol o            | pac            | plu           | taa           | mau           | gra           |
|----------------|---------------|-----------------|------------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|-----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|
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Table 2. Characters used for phylogenetic analysis

0. Average length of adult stage, in microns: (0) small, 200-400 (Fig. 101); (1) medium, 400-600 (Fig. 91); (2) large, > 600 (Womersley 1944: 136, Fig. 1A); (3) very large, > 1600 (Womersley 1944: 137, Fig. 2A).
The states are scored in sequence of increasing length and analyzed as unordered, like all the following multistate characters, to avoid a prejudgement of the plesiomorphic state (e.g. in length).

1. Secondary pattern of granules/lamellae on integumental ridges: (0) absent (Smith Meyer & Ueckermann 1987: 3, Fig. 1); (1) present (Figs. 27, 115).
Grandjean (1939) reported no lamellae in *Terpnacarus*, but I have observed lamellae by SEM in C-segment of a *Terpnacarus* sp. from Finland and e.g. nanorchestids also have lamellae in ridges (Rounsevell & Greensdale, 1988). Ridges are glabrous in *Anystis* and only large primary lamellae of loops and clumps are present in a species ‘sil’ from South Africa (state 2 of character 8, Appendix 3).

2. Secondary pattern granular on integumental ridges: (0) absent; (1) present (Fig. 95); (2) partly granular (Fig. 115).
State 2 suggests that small secondary lamellae develop from small granulae in Bimichaeliini and the structures are considered equivalent. Only granulae are present in *Bimichaelia s.s.*. The character is coded as inapplicable in taxa that have only lamellae, to avoid redundancy.

3. Secondary pattern of small lamellae: (0) absent; (1) present (Fig. 125); (2) partly lamellar (Fig. 115).
State 1 is scored for all the terminals with only small lamellae, i.e. without a mixture of small lamellae and granulae (state 2), although the the lamellae have probably developed independently in Bimichaeliini. Characters 4-6 are coded as inapplicable in taxa that have only granulae.

4. Position of small lamellae on ridges: (0) transverse (Fig. 38); (1) longitudinal.
Transversely inserted lamellae are widespread in Alycidae. Lamellae are longitudinal in a Polynesian species ‘mau’.

5. Density of small lamellae on ridges: (0) sparse (Fig. 142); (1) dense (Fig. 38).
Regarding characters 5 and 6, petralycin lamellae are sparsely situated and uniform in size. The lamellae of *Amphialycus* are also subequal in size but much more densely inserted. Various size classes are present in *Alycus* and *Pachygnathus*.

6. Form of small lamellae: (0) several size classes (Fig. 10); (1) mostly subequal in size (Fig. 73).

7. Primary pattern of large lamellae in clumps or in cells: (0) absent (Figs. 10, 54, 73); (1) present (Figs. 105, 115).
Large lamellae are unique to Bimichaeliinae. Large lamellae of the Bimichaeliinae are three times larger than the small lamellae, and the lamellae of the alycins (cf. Figs. 96 vs. 38) and petralycins (Fig. 142).

8. Form of primary pattern: (0) clumps only (Fig. 110); (1) cells only (Fig. 100); (2) clumps and cells (Appendix 3).
Only one terminal per continent in this material has state 0, and state 2 can be found in an undescribed species ‘sil’ from Africa. State 1 with ± regular polygons reminds me of the globe-like carbon compound C_{60} or fullerene, alias buckyball, as a solution to strengthen the body against collapsing. The mixture of large lamellae (primary pattern) and granulae/small lamellae (secondary pattern of Bimichaeliini) is widespread in the bimichaeliins. The character is coded as inapplicable in taxa that have only lamellae of small size, as defined in character 7.
9. Shape of middorsal cells: (0) ± roundish (Fig. 91); (1) ± polygonal (Fig. 131). The character is coded as inapplicable in taxa which have state 0 of character 8, or large lamellae missing (alycins and petralycins).

10. Dorsal chaetotaxy of adults: (0) holotrichous (Grandjean 1939: 52, Fig. 1); (1) neotrichous (Fig. 26); (2) oligotrichous (Smith Meyer & Ueckermann 1987: 3, Fig.1). Primitive complement of the hairs (28 pairs or holotrichy) may be modified either by reduction (oligotrichy) or increase (neotrichy) in the number of setae (Kethley 1990a). State 1 is the usual type in the adults and nymphs of Alycidae but most of the larvae of alycins, petralycins, *Bimichaelia s.s.t.* and *subnuda*-group, which I have seen, are holotrichous. An exception is the larva of the highly neotrichous *Alycus marinus* (Fig. 40). See also Chapter 1.1.4 for discussion of the possible homoplasy in state 1.

11. Form of shaft of middorsal setae: (0) short (Fig. 105); (1) medium-sized, thin (Fig. 27); (2) long (Smith Meyer & Ueckermann 1987: 3, Fig.1); (3) medium-sized, swollen (Figs. 47, 135). State 1 is the usual type in Alycidae. Shaft is short (state 0) when cilia seem to start from the insertion point directly as in *Bimichaelia s.s.t.*, and long (state 2) when it reaches over a segment as in the outgroup. The shaft is swollen independently twice, in Alycini and in Bimichaelini.

12. Form of dorsal setae on PS-segment: (0) barbed (Smith Meyer & Ueckermann 1987: 3, Fig. 1); (1) pubescent (Fig. 72); (2) sparse basal ciliation (Fig. 101); (3) tapering shaft ciliated (Fig. 141); (4) ± dense ciliation (Fig. 37); (5) scaly (Fig. 121); (6) basal ciliation, shaft scaly (Fig. 19); (7) basal ciliation, shaft barbed (Fig. 115). The character is useful in the grouping of some taxa. E.g. species of *Amphialycus* share state 1 and *Bimichaelia s.s.t.* state 2.

13. Prodorsal sclerotization: (0) absent (Fig. 110); (1) poorly developed (Fig. 100, Appendix 3); (2) strongly developed (Fig. 25). Lamellar pattern differs from that of soft integument only in the sockets and immediate vicinity of the sensilla in state 0, as in the *subnuda*-group. In state 1, large lamellae are in rows (a sign of sclerotization) and in the area between counterparts of sensilla *ve*, as in *Bimichaelia s.s.t.* and an undescribed species *‘sil’*. The sclerotized area extends from the nose to setae in state 2, as in *Petralycus, Alycus, Pachygnathus* and most of *Laminamichaelia*.

14. Form of prodorsal crista from naso to sensillar area: (0) similar to adjacent areas (Fig. 100, Appendix 3); (1) sclerotized, simple (Fig. 8); (2) sclerotized, tripartite (Fig. 130). The crista is hardly sclerotized (state 0) in the species *‘sil’*, and in *Bimichaelia s.s.t.* and the *subnuda*-group (Fig. 110), while state 2 is the usual type in the other Bimichaelini (Fig. 120) and state 1 is shared by *Alycus, Pachygnathus* (Fig. 52) and *Amphialycus* (Fig. 71).

15. Posterior pair of lateral eyes: (0) present (Fig. 12, Smith Meyer & Ueckermann 1987: 3, Fig.1); (1) absent (Fig. 100, Grandjean 1939: 54, Fig. 2). Regarding characters 15-18, one or both pairs of eyes can be lost, reduced (striated lenses) or normal (glabrous), but, when present, the posterior pair is never normal (glabrous) in Alycidae. *Amphialycus* may have also the anterior pair striated (character 18 state 1). The character is coded as inapplicable in taxa which lack the pair of eyes concerned by characters 16 and 18.

16. Form of posterior pair of lateral eyes: (0) lens glabrous (Smith Meyer & Ueckermann 1987: 3, Fig. 1); (1) lens striated (Fig. 12).

17. Anterior pair of lateral eyes: (0) present (Fig. 12, Smith Meyer & Ueckermann 1987: 3, Fig.1, Appendix 3); (1) absent (Figs. 47, 100).
18. Form of anterior pair of lateral eyes: (0) lens glabrous (Fig. 12); (1) lens finely striated (Fig. 75, Appendix 3).

19. Naso: (0) present (Fig. 8); (1) absent (Fig. 25).
A as a rule, in Alycidae this frontal nose-like protrusion is present, flanked by a pair of setae vi (character 21, states 1 and 2), but sometimes lost in Alycus and Amphialycus (Fig. 82).

20. Form of nasal area: (0) finely striated button (Fig. 96); (1) broad flap (Fig. 60); (2) downwards bent proboscis (Fig. 8); (3) naso absent, area normal, i.e. counterparts of setae vi are far apart (Fig. 25); (4) pointed (Fig. 140); (5) cone-like (Alzuet & Delgado 1984: 89, Fig. 7); (6) naso absent, area reduced, i.e. counterparts of setae vi are close to each other (Fig. 82).
Bimichaeliinae and the two Amphialycus studied (Figs. 4 and 68) share state 0; state 4 prevails in petralycins. The area is of importance in diagnosing species of Alycus and Amphialycus.

21. Position of vi: (0) on naso (Grandjean 1939: 52, Fig. 1); (1) on clear microsclerite (Figs. 60, 142); (2) on soft integument (Fig. 106).
Characters 21-34 concern various aspects of prodorsal setae and sensilla. Regarding characters 21-23, a pair of setae vi is always present in Alycidae. With a few exceptions, the pair is similar in length to other prodorsal setae, ciliated, and inserted near naso, on microsclerites (character 21 state 1) in the alycins and petralycins and without microsclerites (character 21 state 2) in the Bimichaeliinae. Setae vi are modified into sensilla in several prostigmatid families (Kethley 1990a).

22. Prodorsal pair of vi: (0) ciliated setae (Fig. 8); (1) sensilla (Smith Meyer & Ueckermann 1987: 3, Fig.1); (2) barbed setae (Fig. 120, Grandjean 1939: 57, Fig. 4C)

23. Length of vi: (0) vi = sce (Fig. 25); (1) vi > sce (Fig. 140); (2) vi < sce (Fig. 82).

24. Form of ve: (0) filamentous sensilla (Fig. 8); (1) capitate sensilla (Fig. 140); (2) baseball bat-shaped sensilla; (3) setae (Grandjean 1939: 54, Fig. 2).
Regarding characters 24-27, a pair of sensilla ve is always present, state 0 is the usual type in Alycidae but state 1 prevails in Petralycini, and the shaft of ve (and sci) is evenly widening towards the apex in an undescribed African species 'clu' (character 24 state 2 and character 27 state 2). The sensilla ve have transformed into setae in several families (Kethley 1990a).

25. Distal part of ve: (0) barbed (Fig. 8); (1) ciliated (Fig. 110); (2) smooth (Fig. 90).

26. Proximal part of ve: (0) barbed (Figs. 8, 94); (1) granular (Fig. 110); (2) smooth (Shiba 1969: 98, Fig. 20A).

27. Form of pair of sensilla sci: (0) filamentous (Fig. 8); (1) capitate (Fig. 104); (2) baseball bat-shaped.
A pair of sensilla sci is always present in Alycidae. Bimichaeliinae have state 1 and, with the exception of one African species 'clu', the other terminals have state 0 in adult forms. Larvae and protonymphs of alycins may have slightly swollen sensilla (Grandjean 1937b, Fig. 4A).

28. Position of pair of setae sce with respect to pair of sensilla: (0) in line with ve (Fig. 8); (1) in line with sci (Grandjean 1939: 54, Fig. 2); (2) posterior to sci (Smith Meyer & Ueckermann 1987: 3, Fig.1).
A pair of setae sce is always present in Alycidae and approximately in line with the anterior pair of sensilla (ve).
29. Position of sce with respect to anterior pair of lateral eyes: (0) above (Fig. 25); (1) anterior (Fig. 36, Appendix 3); (2) eyes absent (Fig. 90).
If the anterior pair of lateral eyes is present, then sce is straight above or slightly anterior to the anterior eye. Petralycins and most of the Bimichaelininae (one African exception 'sil') have no eyes.

30. Prodorsal pair of setae exp: (0) absent (Fig. 140); (1) present (Fig. 8, Appendix 3).
Regarding characters 30-32, the pair of setae exp is absent in Petralycus, reduced in size (less cilia) and above either posterior or anterior pair of lateral eyes in Alycus, Pachygnathus and Amphialycus (character 31 state 0, character 32 states 1 or 2). When the eyes are absent, as in the Bimichaelini, the setae are normal in size on rim (character 31 state 1, character 32 state 2). In an African bimichaeline species 'sil' with a pair of eyes, a normal-sized seta is above an eye.

31. Form of pair of exp: (0) small in size (Fig. 25); (1) like other setae (Fig. 100, Appendix 3).

32. Position of pair of exp: (0) above posterior pair of lateral eyes (Fig. 25); (1) above anterior pair of lateral eyes (Fig. 36, Appendix 3); (2) on rim (Fig. 100).

33. Form of pair of setae in: (0) ciliated (Fig. 8); (1) pubescent (Fig. 71); (2) barbed (Grandjean 1939: 61, Fig. 6); (3) scaly (Fig. 120); (4) absent (Theron 1977: 43, Fig. 16).
Caudal setae and setae in often resemble each other, which is useful in the identification of e.g. the genus Amphialycus (Fig. 72, character 12 state 1, character 33 state 1).

34. Number of setae and sensilla on prodorsum: (0) ≤ five pairs (Figs. 140, Theron 1977: 43, Fig. 16); (1) six pairs (Fig. 25); (2) seven pairs (Fig. 60); (3) additional setae only on soft integument (Fig. 120); (4) additional setae on soft and hard integument (Fig. 130).
The primitive number of prodorsal setae is 6 pairs (Kethley 1990a) and state 1 is the usual type in Alycus, Pachygnathus, Amphialycus, Bimichaelia s.s. and the submuda-group. An additional seta has appeared only once on the sclerotized prodorsal area (state 2) in the alycins studied here, and seta exp is obviously lost in an Australian species (not included in the analysis). States 3 and 4 are the usual types in Laminamichaelia and the number can increase to dozens due to neotrichy in some tropical Bimichaelini.

35. Structure of chelicera: (0) robust, short (Fig. 2); (1) robust, elongated (Fig. 4); (2) beak-like (Fig. 3); (3) stylet-like (Fig. 123, Appendix 3); (4) hook-like (Smith Meyer & Ueckermann 1987: 3, Fig.7).
Regarding characters 35-40, the shape of the chelicera is difficult to interpret from slide-mounted specimens and the fine structure of the chelicera is insufficiently known. The primitive chelate-dentate type in the alycins is with a few teeth both in outer and inner edges of the chelae and a deep notch apically (Fig. 14) to which petralycins have added a couple of teeth (Fig. 143). Bimichaelininae have lost their outer teeth (Fig. 119, character 36 state 0), but the inner teeth are present (character 37 state 3) and the stylets have a groove (character 38 state 1). Variation in the Bimichaelininae stylets and the detailed structure, position and number of the teeth, should be studied routinely using SEM in order to properly assess the states of characters 35 and 37 for phylogenetic analyses.

36. Lateral edges of cheliceral digits: (0) outer edges smooth (Fig. 122); (1) teeth on outer edges (Figs. 14, 63, 143).

37. Form of cheliceral digits: (0) a few large teeth on outer edges (Fig. 14); (1) a few minute teeth on outer edges (Fig. 63); (2) several teeth on outer edges (Fig. 143); (3) teeth on inner edges, outer edges smooth (Fig. 122); (4) terminal hook (Smith Meyer & Ueckermann 1987: 3, Fig.7).

38. Inner surface of cheliceral shafts: (0) flat (Figs. 2, 3, 4); (1) with groove (Fig. 124).
39. Number of cheliceral setae: (0) two (Fig. 41); (1) one (Fig. 2, Appendix 3); (2) absent (Fig. 3).
State 1 can be found in Alycus, Amphialycus and one African Bimichaeliinae species 'sil'. The remaining Bimichaeliinae, Pachygnathus and the Petralycini possess state 2. State 0 prevails in the outgroup (Smith Meyer & Ueckermann 1987: 3, Fig.7) and the sister group (Grandjean 1939: 55, Fig 3D), and, primitively, the number is probably two, but neotrichy is also a possibility in the highly neotrichous Alycus trichotus.

40. Position of cheliceral setae: (0) dorsal (Fig. 2, Appendix 3); (1) abaxial (Fig. 4); (3) adaxial (Grandjean 1939: 55, Fig. 3D).
Alycus and an African Bimichaeliinae species 'sil' have state 0 and all the Amphialycus studied here have state 1. The character is coded as inapplicable in taxa which have not the cheliceral setae.

41. Form of rutellum: (0) well developed, with ventral lobes (Fig. 16); (1) well developed, with distal lobes (Fig. 70); (2) small, with tiny distal lobes (Fig. 58); (3) absent (Fig. 123).
Rutella are a pair of elongated projections, inserted on both sides of the mouth opening (Fig. 29) and obviously have a role in feeding. Their structure is different in different families. Lobes are membraneous or flap-like parts of this transformed seta. State 0 is the usual type in Petralycus and Alycus, state 1 in Amphialycus and state 2 in Pachygnathus. The bimichaeliines have lost their rutella (state 3).

42. Subcapitulum: (0) short (Fig. 29); (1) elongated (Figs. 92, 102).
State 1 in the Bimichaeliinae is obviously connected with the elongation of their chelicera into stylets (character 35 state 3).

43. Number of genital setae: (0) < 10 (Fig. 107); (1) 10-30 (Fig. 6); (2) > 30 (an undescribed Polynesian species 'mau').
The character is divided into states so that the intraspecific variation of all terminals is within the limits of the states defined, i.e. no terminal is polyphyletic. State 1 is the usual type in Alycidae but state 0 can be found in Bimichaelia s.st. and setigera-group and subnuda-group.

44. Position of palpal solenidion: (0) dorsal, alike others (Fig. 85); (1) dorsal, reaching over apical end (Fig. 145); (2) apical (Fig. 97).
State 0 is the usual type in Alycus, Pachygnathus and Amphialycus, state 1 is known in the Petralycini and state 2 in the Bimichaeliinae only.

45. Form of palpal eupathids: (0) pseudacanthoids (Fig. 18); (1) TP-type (Fig. 97); (2) acanthoid (Smith Meyer & Ueckermann 1987: 3, Fig.6); (3) mucronate (Fig. 145).
Various forms of chemoreceptors apically and ventrally on appendages, called eupathids, are modified setae having a hollow core and an enlarged alveolus (Kethley 1990a). Some cilia are still present in state 0 in the alycins, barb-like remnants of cilia in stiff shafts in state 3 in Petralycus, cilia are absent in state 2 in the outgroup and there is a terminal pore in state 1 in the Bimichaeliinae.

46. Position of eupathids: (0) free (Fig. 18); (1) basally fused (Fig. 85); (2) one supporting solenidion (Fig. 97); (3) two supporting solenidia (Fig. 119).
Distal eupathids on palpal tarsus have state 0 in the alycins and petralycins. Their usual number of six can be reduced to four or two. Their mutual distances vary in Amphialycus and ultimately they can be fused (state 1) in A. (Orthacarus) oblongus. In the Bimichaeliinae the apical solenidion is ventrally supported by either both eupathids (state 3), or just one of them (state 2).

47. Form of legs I: (0) equal in size to other legs (Figs. 6, 91); (1) enlarged (Fig. 146).
State 0 is the usual type in Alycidae and state 1 is known in petralycins only.

48. Femora IV: (0) divided (Fig. 7, Appendix 3); (1) undivided (Fig. 112).
State 1 is the usual type in Bimichaeliinae, state 0 is only known in one undescribed bimichaeliine species 'sil' studied here and in the rest of the terminals in Alycidae.
49. Trochanter IV: (0) normal (Fig. 6); (1) elongated (Fig. 7).

50. Space of soft integument between coxisternae II: (0) wide (Fig. 6); (1) small (Fig. 7).

51. Presence of eupathids on tarsus II: (0) absent; (1) present (Fig. 134, Smith Meyer & Ueckermann 1987: 5, Fig. 12).

Eupathids are hollow setae situated ventrally and apically on the tarsus. Eupathids are commonly present on tarsi I (Grandjean 1939: 59, Fig. 5A), but state 0 is the usual type in alycins and petralycins while state 1 is known in Bimichaeliinae and Anystis.

52. Number of eupathids on tarsus I: (0) a few (Fig. 99); (1) many (Grandjean 1943: 13, Fig. 8).

State 1 is known in Amphiyalicus and in Petralycini.

53. Form of empodia on adults: (0) with a claw (Fig. 31); (1) clawless (Fig. 99).

The empodium is an unpaired structure between the two tarsal claws. Bimichaeliinae and Petralycini have state 1 and state 0 is present in the adults of the Alycini, see Chapter 3.1, Lineage VI.

54. Number of empodial setulae: (0) a few (Fig. 65); (1) plenty (Fig. 81).

Setulae are small, seta-like cuticular processes, attached to the shaft of empodium. State 1 is present in Amphiyalicus, Bimichaeliinae (Fig. 99) and Petralycini (Theron 1977: 44, Fig. 27). Alycus (Fig. 31) and Pachygnathus have state 0.

55. Form of small solenidia: (0) claviform (Fig. 147); (1) baculiform (Fig. 148); (2) ceratiform (Fig. 56).

Regarding characters 55-59 in Alycidae, the various forms of chemoreceptors situated dorsally on legs, called solenidia, fall roughly into two size categories (Figs. 88, 136). When simultaneously present on a segment, small solenidia are usually slimmer, different in form (ceratiform/piliform) and more basally inserted than the large, baculiform solenidia (not always, Fig. 137). The number of solenidia in both size categories varies intraspecifically, but the variation is higher and more common in small solenidia.

56. Number of large solenidia on tibia I: (0) two (Fig. 114); (1) one (Fig. 56, Appendix 3).

State 1 is present in the alycins, petralycins, Bimicialia s.st. and an undescribed species ‘sil’. Most of Bimichaeliinae show state 0.

57. Position of two large solenidia on tibia I: (0) one distal only (Fig. 56); (1) far apart (Fig. 123); (2) side by side (Fig. 114).

When the insertion points are far apart (state 1), they can either be aligned (an undescribed species ‘ful’ from North America), or more or less obliquely.

58. Form of large solenidia on tibia I: (0) one claviform (Fig. 147); (1) one baculiform (Fig. 149, Appendix 3); (2) one ceratiform; (3) two baculiform (Fig. 114).

The names of the solenidial types are explained earlier in this Section 2.4. State 0 is observed in two closely related, primitive petralycins (unicorns from Europe and ‘pet’ from North America), whereas the other petralycins, alycins, Bimichaelia s.st. and an undescribed bimichaeliine ‘sil’ possess state 1. State 2 is unique to an undescribed bimichaeliin species ‘mau’ from Polynesia. When two solenidia are present, though baculiform, their thickness may differ (state 3).

59. Presence of large (or baculiform) solenidia on tarsi, tibiae, genua and femora I II III IV, respectively: (0) all solenidia ± swollen in middle/claviform or baculiform (Figs. 147, 148, 149); (1) all solenidia ± ceratiform (Fig. Grandjean 1939: 59, Fig. 5A); (2) 1100 1110 0100 0000 (Fig. 5); (3) 3200 1111 0000 0100 (Fig. 98); (4) 2200 2221 0100 0000 (Figs. 113, 114, 116, 117, 118); (5) 2200 2221 0100 0100 (Figs. 123, 126, 128); (6) 3200 2220 0100
Both large and small solenidia are similar in form in each of the Petralycini species (state 0). The number of large solenidia per leg segment is constant in Alycus, Pachygnathus and Amphialycus (state 2) but varies interspecifically a lot in the Bimichaeliinae (states 3-8). Different patterns characterize Bimichaelia sensu stricto (state 3), the subnuda-group (state 4), the setigera-group (state 5) and the arbusculosa-group (state 6). An undescribed species ‘sil’ from Africa (state 7), an extremely neotrichous species ‘mau’ from Polynesia (state 8), and a species ‘gra’ from Southeast Asia (state 9) show unique solenidial patterns, suggesting that Bimichaeliinae evolution may have been more complicated than indicated by the analysis.

Drawings of these mites and their organs can be found in several text-books, such as Evans et al. (1961), Krantz (1978), van der Hammen (1989), Kethley (1990a), Evans (1992), Alberti & Coons (1999), Walter & Proctor (1999) and Krantz & Walter (2009). The image of an organ by SEM becomes evident in the Figure indicated in the list of the characters below. The character in question may be visible in several other figures as well, with or without indication marks. The uniform notations proposed for various organs of Prostigmata and the abbreviations used in the figures are adopted mainly from Kethley (1990a).

Abbreviations for characters:
AD, adanal (7th opisthosomal) segment, Fig. 26
ad, adoral seta, Fig. 16
AN, anal (8th opisthosomal) segment, Fig. 26
An, anal plates, Fig. 7
BFE, basifemur, Fig. 28
C, first opisthosomal segment, Fig. 26
Ch, chelicera, Fig. 29
cha, posterior cheliceral seta, Fig. 36
chb, anterior cheliceral seta, Fig. 4
cx, coxalfield, Fig. 6
D, second opisthosomal segment, Fig. 26
δ (delta), dehiscence line, Fig. 40
E, third opisthosomal segment, Fig. 26
ε (epsilon), famulus, Fig. 127
el, supra Coxal seta of leg I, Fig. 82
ep, supra Coxal seta of palpus, Fig. 82
exp, posterior exobothridial seta, Fig. 8
F, fourth opisthosomal segment, Fig. 26
FE, femur, Fig. 114
GE, genu, Fig. 114
Gen, genital valves, Fig. 7
H, fifth opisthosomal segment, Fig. 26
ia, cupule of segment D, Fig. 40
in, interlamellar seta, Fig. 8
k' and k", palpal eupathids, Fig. 97
LA, labrum or upper lip, Fig. 29
LI, labium or under lip, Fig. 29
LL, lateral lip, Fig. 29
ly, lyrifissure, Fig. 108
Na, naso, Fig. 8
3. Results

3.1. Results of the phylogenetic analysis

The parsimony analysis produced 1513 shortest cladograms, the strict consensus cladogram of which (232 steps, CI 54, RI 87) was reasonably well resolved except for some polytomies in the clades that included *Amphialycus, Pachygnathus, Bimichaelia* and *Laminamichaelia* (Fig. 1). The mutual arrangement of the clades IX, X and XI remained unsolved. Excluding the clade IX (*Amphialycus*) and clade X (*Pachygnathus*), the rest of terminals of the clade VI form three clades, but splitting of the species into three new genera seems unfounded, premature, and it would be worse of the two alternatives. The species are traditionally included in the genus *Alycus*, and whether it is a monophyletic group or not, remains unsolved on basis of the characters used in this time. Neither can monophyly or non-monophyly of the family Alycidae be demonstrated because one or more clades within this group cannot be shown to be more closely related to other mites than they are to other members of Alycidae, in lack of such other mite groups in this analysis. However, the results suggest that the apomorphies, proposed for the *Bimichaelia/Petralycus* cluster by Lindquist & Palacio-Vargas (1991), are independently born. The large number of tropical Bimichaeliinae species, still insufficiently examined, obstructs the view on internal relationships of the subfamily. The final classification must be left until a worldwide inventory and revision of the genera is made. The dicotomy between the two basal clades and the consequent four major clades were supported by character state changes listed below.
Fig. 1: Phylogeny of Alycidae. Strict consensus tree (232 steps, CI 54, RI 87) of the 1513 most parsimonious cladograms obtained with the program NONA. Numbers above hashmarks (open = homoplasious, black = unique) refer to characters, numbers under hashmarks refer to state changes to the state indicated. Only unambiguous changes are shown.
Subfamily and tribe ranks have been proposed for these clades because they form diagnostically distinct units, but only the (three) tribes present in Europe are defined below. The minor monophyletic clades with generic status are defined in detail in the systematic parts of the study for Bimichaeliini and Alycini.

**Lineage I. Alycidae G. Canestrini & Fanzago, 1877** This family can be defined by at least one progressive and one regressive state.

11/1. **Presence of middorsal setae with medium-sized shafts (Fig. 27).** This is a primitive state and shafts can either be shortened (*Bimichaelia* Fig. 105) or elongated (Smith Meyer & Ueckermann 1987: 3, Fig.1).

12/4. **Presence of ± dense ciliation on shafts of caudal setae (Fig. 37).** High number of cilia from top to toe may be an apomorphic state but form and number of cilia are transformed several times by either reduction or adding of cilia in Alycidae.

23/0. **Equality in length of prodorsal setae vi and sce (Fig. 25).** This is a plesiomorphic state and especially the setae vi can be either elongated (Fig. 36) or reduced (Fig. 82) more.

24/0. **Presence of filamentous prodorsal sensilla ve (Figs. 8, 100).** Prodorsal sensilla are supposed to be filamentous in the origin.

39/1, 2. **Presence of one or none cheliceral setae (Figs. 2, 3, 102, 143).** Two pairs of cheliceral setae present in the outgroup and sister group may indicate a plesiomorphic state in Acari. The most primitive alycins have only one pair which is independently lost in *Pachygnathus* and most of the Bimichaeliinae. The second pair in *Alycus trichotus* is probably additional.

**Lineage II. Bimichaeliinae.** This basal group can be defined by eight progressive and one regressive states.

7/1. **Presence of large lamellae in rosettes and/or in clumps (Figs. 100, 101, 110, 111).** Enlarged lamellae are unique to this lineage. An undescribed species ‘sil’ from South Africa has both rosettes and clumps and subnuda-group only clumps. Primitively the cells of the rosettes are roundish, but see arbusculosa-group.

27/1. **Clavation of the prodorsal posterior sensilla sci (Figs. 90, 104).** Distension of the distal parts of the pair of sensilla sci can also be found in other groups, e.g. Tydeoidea, Heterostigmata and oribatids.

31/1. **Similarity of setae exp with other prodorsal setae (Figs. 90, 100, 110, 120, 130, Appendix 3).** Setae exp cannot be recognized and named if the prodorsum is neotrichous, but when holotrichous (or the neotrichy is restricted to in-area as in an undescribed species ‘sil’), the pair is the proximal one of the laterally inserted setae. The pair exp is smaller (less ciliated) than the other setae in Alycini and missing in Petralycini.

35/3, 37/3, 38/1. **Presence of a groove on inner side of stylet-like cheliceral shafts and teeth on inner edges of digits (Figs. 122, 123, 124).** When adjusted together, a tube can be constructed of the two half-pipes suggesting a model of perhaps the most primitive sucking apparatus ever. Chelicerae have elongated in *Pachygnathus* of Alycini (Fig. 3), too, but are not thinned into stylet-like structures. The outer edges of these ‘styles’ are smooth but there are ‘teeth’ in the outer edges on Petralycini and Alycini. In addition there may be a row of numerous obliquely inserted flap-like projections on the inner surface of movable digits of the bimichaeliids reported also as teeth e.g. by Grandjean (1943). Lumping together with predators is not a unique phenomenon in the mite taxonomy (cf. Gerson, 1972), but these cheliceral structures strongly suggest the Bimichaeliinae not having so close relationship with the two other major groups.
42/1. **Elongation of subcapitulum (Figs. 92, 102).** Elongation of the proper subcapitulum and especially lateral lips is unique to this lineage among Alycidae. This elongation together with the complete loss of rutellar setae (41/3, when present, inserted laterally on subcapitulum) are obviously in connection with the transformation of chelicera discussed above.

44/2. **Position of palpal solenidion apically (Fig 97).** The insertion of the solenidion at the tip of palpal tarsi is unique to the lineage. The solenidion is inserted dorso-distally on palpi of Alycini and Petralycini.

45/1, 46/2. **Presence of solenidia-supporting TP-type eupathids on palpal tarsi (Figs. 97, 119).** Also petralycids have one pair of eupathids on palpi but the terminal pore or TP-type (Evans, 1992) and the close contact with solenidion is unique to this lineage.

51/1. **Presence of eupathids on tarsi I and II (Fig. 134).** Eupathids are present also in Alycinae but only on tarsi I.

**Lineage III. Alycinae.** The node of this sister-group of Bimichaeliinae was supported by three character state changes considered to be of early derivation by nature and there is a strong possibility that they have developed independently in the Petralycini and Alycini.

3/1. **Presence of secondary pattern on ridges of skin by small lamellae (Figs. 10, 27, 38, 54, 62, 73, 84, 142).** Petralycid lamellae are sparsely situated and uniform in size. Similar lamellation can also be found in another family, Nanorchestidae (Rouncevell & Greensdale, 1988). Lamellae of *Alycus* and *Pachygnathus* are of various size classes and lamellae of *Amphialycus* are much more densely situated compared to the lamellae of Petralycini. Small lamellae develop from small granulae on Bimichaeliinae (Figs. 95, 115) which suggests the ridges being smooth in the origin. Lamellae of the main lineages may have been developed convergently.

14/1. **Presence of sclerotized crista (Figs. 8, 25, 36, 47, 52, 60, 71, 82, 140).** The area from naso to anterior sensilla is variably hardened. The band may even be suddenly crossed by a soft strip (Fig. 25). The sclerite is evenly constructed, not tripartite like on Bimichaeliinae (Figs. 120, 132). Prodorsal integument must have had a strong tendency to strengthen itself in order to stabilize the sensillar area. Missing or weakness of the sclerotization of *Bimichaelia* and *subnuda*-group (Figs. 90, 100, 110) suggests independent hardening on Bimichaeliinae and this might be the case in the Petralycini and Alycini as well.

41/0. **Presence of well developed rutella (Figs. 16, 29, 33, 44, 49, 58, 66, 74, 144).** Transformation of an anterior pair of setae on both sides of chelicerae of these predators into lobed rutella (e.g. for cleansing purposes) can also be seen as a plesiomorphism.

**Lineage IV. Bimichaeliini new tribe.** This sister-group of a monotypic African tribe includes all the rest of the Bimichaeliinae. It can be defined by one regressive and two progressive states. The African unnamed ‘living fossil’ (*sil*) will be properly described and correctly published after this study in collaboration with Prof. Pieter Theron. Some selected figures of the species for comparison are in Appendix 3.

17/1. **Loss of anterior pair of lateral eyes (Figs. 90, 100, 110, 120, 130).** Presence of the lateral setae *exp* and *sce* above the anterior pair of lateral eyes (as in Alycini) in the sister group from South Africa, along with other primitive character states, indicates that the eyes are not of secondary origin and suggests that eyelessness has arisen independently among Alycidae on several occasions. The presence of eyes has previously been reported twice. I have not seen any material of the Asian *B. reticulata* described by Shiba (1969),
while *B. sylvestrana* from South America described by Berlese & Leonardi (1901) have no eyes but glittering crystal-like corpuscles beneath prodorsal (and dorsal) skin instead.  

32/2. **Presence of pair of setae exp on rim of prodorsum (Figs. 90, 100, 110).** Setae *exp* cannot be individually pinpointed on soft integument of prodorsum if additional setae are numerous (Figs. 120, 130).

49/1. **Presence of undivided femora IV (Fig. 112).** Primitively, the division of femora IV into basifemora and telofemora (e.g. Fig. 28) is still present in the Petralycini, Alycini and an unnamed Bimichaeliinae ‘*sil*’ from South Africa (Appendix 3).

**Lineage V. Petralycini new tribe.** The major group in question can be defined at least by seven progressive and two regressive states.  

12/3. **Presence of sparse ciliation on tapering shafts of caudal setae (Fig. 141, 150).** The outgroup have long and barbed setae but it may be that, primitively, the dorsal setae were ciliated with tapering shafts like also the setae in Alycini are, and this kind of sparse ciliation along the way represents early derivation.  

17/1. **Loss of anterior pair of lateral eyes (Fig. 140).** The pair of eyes is independently lost in Lineage IV and *Alycus marinus* (but still present in all other members of Lineage III).

24/1, 26/1. **Clavation of the prodorsal anterior sensilla ve (Fig. 140).** Distension and becoming sparsely barbed distally, and with proximal granulation, of the originally filamentous pair of sensilla *ve* is unique to the lineage.  

30/0, 34/0. **Reduction in the number of structures of setal origin on prodorsum because of the loss of pair of setae exp (Fig. 140).** The seta *exp* is missing already in the most primitive petralycins and also the pair of setae *in* may be lost. This can be considered as a loss and regression, the primitive number of prodorsal setae being six pairs (Kethley 1990a). In Bimichaeliinae the pair of setae *exp* does not differ in form from the other setae while in Alycini they are smaller than the others. The pair of fundamental setae *exp* is also absent in an Australian species (Prof. Walter, in litt.) which is probably *Alycus occidentalis* (see Chapter 2.3).

35/1, 37/2. **Presence of several teeth on outer edges of robust and elongated chelicera (Fig. 143).** Chelicerae have elongated independently into beak- and stylet-like structures with slim stalks in *Pachygnathus* (Alycini) and Bimichaeliinae and, in spite of elongation, have retained their robustness in *Amphialycus* (Alycini) and Petralycini. Alycini also have dentate outer edges of digits, but with the addition of one or two strong teeth, especially the outer edges of the fixed digit are unique to this lineage.  

44/1, 45/3. **Stretching of palpal solenidion across the apical end and over the mucronate eupathids (Fig. 145).** Dorsally inserted solenidion yet partly covering distal eupathids is unique to this lineage. Bimichaeliinae also have only one pair of palpal eupathids but they have a terminal pore apically (TP-type) and the transformation of apical setae into a pair of stiff eupathids is unique to this lineage. Alycini have two or more pairs of pseudacanthoid type.  

47/1. **Hypertrophic first pair of legs (Fig. 146).** The forelegs of petralycins have become longer and thicker than the other pairs of legs.  

52/1. **Presence of numerous eupathids on tarsi I (Figs. 8B in Grandjean, 1943 and 12, 23 in Theron, 1977).** Several setae on ventral side of tarsi I have also transformed into eupathids in *Amphialycus*.

55/1. **Presence of small solenidia having the same diameter from one end to the other (Figs. 147-149).** Baculiform, ceratiform and piliform solenidia prevail in both the Alycini and Bimichaeliinae, whereas only claviform and baculiform solenidia can be found on
Holarctic petralycins. Thinning is manifested in the South African petralycins but not the tapering (Figs. 148, 149), hence the small solenidia also have a baculiform appearance. The most primitive petralycins have claviform solenidia only. This suggests that separation of the Petralycini should have happened before the solenidial evolution, proposed by Grandjean, started (see Chapter 9.2.1). Thus thinning and a baculiform morphology of small solenidia appeared independently twice.

Lineage VI. Alycini new tribe. This major group can be defined at least by one progressive and two regressive states.

6/0. Presence of small lamellae in several size classes (Figs. 10, 27, 38, 54, 62). Small lamellae are probably born independently in the main lineages (see Lineage III, 3/1 above). Adjacent lamellae differ in size whereas in *Amphialycus* they are subequal (Figs. 73, 84).

17/1. Presence of striated posterior pair of lateral eyes (Figs. 12, 47, 75). Alycini still have retained a striated vestige of the pair of eyes which is completely lost in the other groups involved.

53/0, 54/0. Presence of unguiculate empodium with a few setulae on all legs of adults (Figs. 31, 65, 81). OConnor (1982, p. 129) suggests a pad-like empodium to be an ancestral condition, and an empodial claw-like hook is missing from the fourth pair of legs in larvae and protonymphs, which could also be used as a good cause to keep the presence of hooks as derived (Kethley, 1990a, p. 674). However, Lindquist & Palacios-Vargas (1991) consider this state plesiomorphic. Empodia are without an apical hook in the Petralycini and Bimichaeliinae (Figs. 91, 99). Number of setulae is increased independently in *Amphialycus* (Fig. 81) and Bimichaeliiini (Fig. 99) and Petralycini (Theron 1977: 44, Fig. 23).

62/1. Presence of characteristic patterning of large (baculiform) solenidia (Figs. 5, 80, 88, 89). One thick (or ± baculiform) solenidion per Ta I, Ta II, Ti I, Ti II, Ti III and Ge II is constant and considered plesiomorphic by earlier authors. The numbers of large solenidia may vary due to neotrichy (e.g. Figs. 108 vs. 109) in other major groups. Also one of the small solenidia is slightly swollen on Ti I of highly neotrichous *Alycus marinus* (Fig. 51).

3.2. Key to the subfamilies and tribes of Alycidae

Presence of two pairs of prodorsal sensilla (*ve* and *sci*) inserted in separate bothridia (cf. Lordalycidae with a communal depression for *ve*) is the most convenient way to recognize members of endeostigmatic Alycidae. This character state is also present in two other families: Proterorhagidiidae and Nanorchestidae. Proterorhagidiidae differ from Alycidae in having unusually enlarged, rhagidiid-like chelicera, which are at least one-third as long as idiosoma, and the movable finger about 0.5 as long as the entire chelicera (compare with Figs. 6, 112 and 141 for Alycidae). Nanorchestidae differ in having only one claw per leg (vs. two or three in Alycidae, see Figs. 81, 91, 146). Kethley (1990a) listed also seven prostigmatic families with two pairs of sensilla (*vi* and *sci*), but either their palpi have claw-like seta (not straight) or their chelicerae are hooked (not chelate). Other characters important in the description and identification of Alycidae are listed in Chapter 1.1.2. Kethley (1982) recognized seven genera in the cluster. Womersley (1944) created two subfamilies (Alycinae and Bimichaeliinae) mainly on grounds of differences in cheliceral structure, without being aware of *Petralycus*. The proposed tribe for petralycins also has a unique cheliceral structure. Yet occasionally, the chelicerae are invaginated and
difficult to see and the sensilla lost. Therefore both the sensilla, which in practice are always observable, and the chelicerae have been used for the conventional key. All the European Bimichaeliinae studied have granulæ/small lamellae (secondary pattern) on their skin but the pattern may also be absent. The tribes are defined below in the revisional chapters 4, 5 and 6 on their European members.

1. – Large lamellæ present (Fig. 132), posterior pair of sensilla globular (Fig. 100), chelicera stylet-like (Fig. 123) …Bimichaeliinae
   - Secondary pattern present (Figs. 105, 125), eyes absent (Fig. 110), femora IV undivided (Fig. 112) …Bimichaelini
2. – Large lamellæ absent, small lamellæ present (Fig. 38) …Alycinae
   - Anterior pair of sensilla globular (Fig. 140), chelicera robust, elongated (Fig. 143) …Petralycini
   - Both pairs of prodorsal sensilla filamentous (Fig. 8), chelicera robust, short (Fig. 2), beak-like (Fig. 3) or robust, elongated (Fig. 4) …Alycini

4. Taxonomy of European Alycini

4.1. Introduction

Thirteen of the fifteen nominal species of the old generic complex Pachygnathus/Alycus has been described from Europe or a nearby (former) colony in northern Africa and, traditionally, distributed into four genera. The description of the Pachygnathe velu Dugès, 1834 (Pachygnathus villosus Oken, 1836) from France, together with the description of Alycus roseus Koch, 1842 from Germany, are the oldest ones and much disputed. At the beginning of the 20th century Trägårdh (1909) and Halbert (1920) described Alichus rostratus and Alicus oblongus from Sweden and Ireland, respectively. In a series of papers Grandjean (1936-1937) defined Pachygnathus dugesi, P. ornithorhynchus and P. leucogaster from France and P. trichotus from Algeria. He also described a new subspecies, P. dugesi denasutus from Strasbourg and suspected some of the French alycins not to be new to science. Nonetheless, he made good-quality descriptions of most of them. Van der Hammen (1969) synonymized P. dugesi with A. roseus and established two more subspecies, A. roseus roseus from Germany, The Netherlands and the North of France plus A. roseus dugesi from Dordogne, where Grandjean used to live. Zachvatkin (1949) described Amphialycus pentophthalmus and Orthacarus tremli from the Ukraine and transferred P. leugocaster into Amphialycus. Bottazzi (1950a, 1950b) proposed Pachygnathus berlesei and P. lombardinii from Italy and Willmann (1953) P. arhinosus from Austria. Some years later, P. marinus Schuster, 1958 from the Mediterranean littoral zone in France was published. So far, only Alycus occidentalis Womersley, 1944 and Pachygnathus selvaticus Alzuet & Delgado, 1984 have their type localities far from this continent, but passing remarks have been made on several undescribed species outside Europe (Krantz, 1978; Theron, 1979; Walter, 1988).

In this work, nine species in three genera are recognized in Europe. Both of the old generic names are retained as valid, Pachygnathus being adopted for the group of species with long, beak-like chelicera in the tribe.

The original description of Pachygnathe velu by Dugès, 1834 (Pachygnathus villosus by authors) is enigmatic but the species-name of the type species of the genus can be preserved by considering it as a senior synonym of the well-described P. ornithorhynchus Grandjean, 1937. The specific name Alycus roseus C.L. Koch, 1842 should be used for the
relatively common lilac species, redescribed as *Alycus roseus* by van der Hammen (1989) and as *Pachygnathus dugesi* by Grandjean (1937a) from West European material. *A. denasutus* is raised to species level whereas the other two subspecies are rejected here. *Orthacarus* is reduced to subgeneric status under *Amphialycus*.

### 4.2. Alycini G. Canestrini & Fanzago, 1877 new rank

**Tribe Alycini G. Canestrini & Fanzago, 1877**

Alychni G. Canestrini & Fanzago, 1877: 168, misspelling for Alycini, based on *Alycus*.


Aelicidae Thor, 1925: 263, in part (*Alycus* only); Thor, 1929: 185, pls. 6–7, trees, in part (*Alycus* only); Womersley, 1944: 133, in part (*Pachygnathus = Alycus* only); Judson, 2000: 533, in part (alycins only). Pachygnathidaidae Kramer, 1877: 234 (not Menge, 1866), based on *Pachygnathus*; Grandjean, 1939: 3, in part (*Pachygnathus = Alycus* only); Zachvatkin, 1949: 292, augmented *Orthacarus* and *Amphialycus*.

Bimichaelidae Kethley, 1982: 118, in part (alycins only), erroneous orthography.

Bimichaeliidae OConnor, 1984: 22, in part (alycins only); Kethley, 1990a: 670, key, in part (alycins only).

See also synonymy under Alycidae in Chapter 1.1.1.

**Type genus: Alycus C.L. Koch, 1842**

The detailed description of *Pachygnathus* sensu Grandjean (1936–1937, 1943) was based on four French species and the delineation (of *Pachygnathus s.l.*) corresponds to the definition of the tribe Alycini. In addition to nine European species described below, species from Australia, South Africa and North America have been reported, see Remarks (25), Unchecked sub *Alycus* and Remarks (6), respectively. All the world members examined by me and described so far have been taken into account in the modified description below.

**Differential diagnosis.** The tribe Alycini can easily be segregated from the tribes of Bimichaeliini and Petralycini, as well as from the rest of the Endeostigmata, by the presence of rudimentary posterior pair of lateral eyes, two pairs of filamentous sensilla, and chelate chelicerae with three to four teeth each.

**Description.** Small to medium-sized (500 ± 200 μm); colour white to reddish-violet; hysterosoma soft, segmented, usually neotrichous on adults; integumental ridges densely covered by transverse lamellae; dorsal setae colourless, plumose; prodorsum sclerotized (Fig. 60): anterior pair of lateral eyes usually present, posterior pair of lateral eyes rudimentary, sclerotized bosses just behind the anterior eyes, naso either a fingertip-like projection directed downwards, flap-like, button-like, or missing; six (rarely seven or five) pairs of setal elements on prodorsum, setae *exp* reduced (smaller in size) in comparison to other setae, sensilla *ve* and *sci* filamentous; gnathosoma (Fig. 29): chelate-dentate chelicera (Figs. 2–4) robust and short, robust and elongated, or basally bulbous but distally thin and elongated onto beak-like elements - always with only a few teeth on outer edges of cheliceral digits, cheliceral setae two, one or zero pairs; subcapitulum normal (not elongated): rutella present, adoral setae one to three pairs, smooth; palpal tarsi (Fig. 55) with four to six eupathids of pseudacanthoid type, one baculiform solenidion dorsally, and a lyriform fissure proximally, a pair of supracoxal setae (*ep*) present on dorsal bases of palpi (Figs. 4, 82); legs in two groups (Figs. 6, 7), a pair of supracoxal setae (*el*) present on dorsal bases of legs I (Figs. 52, 82), femora IV divided into telofemur and basifemur,
Members of Alycini are early derivative mites with plenty of plesiomorphic characters. The group was originally based on Alycus/Pachygnathus s.l. Grandjean (1936) emphasized that the species in his small collection were very distinct and based his separation of four species of Pachygnathus (sensu lato) on structures linked to feeding behaviour. Since then, new species, some closely related to the Grandjean’s species, have been separated on basis of differences in prodorsal and pedal sensory organs and new genera have even been proposed for the species (Zachvatkin 1949). As mentioned earlier, Grandjean's (1936-1937, 1943) diagnosis of Pachygnathus s.l. also is applicable to the Alycini. Because members of all the presently recognized genera (Alycus, Pachygnathus, and Amphialycus) are represented in the European fauna, it seems pertinent to re-evaluate and redefine the old generic taxa, based on SEM examination of the character states of the species.

In general, the specific separation of alycins is based on details of the nasal area; the form and position of prodorsal setae; the number of cheliceral and adoral setae; and major differences in solenidial numbers.

Characters used for the generic separation of alycins can be found in the construction of the dorsal integument; the form of the chelicera and rutella; the number and form of eupathids on palpal tarsi; the size of coxisternal plates II; and the number of empodial setules.

4.3. Key to the genera and species of Alycini

The following three groups within Alycini were obtained from the analysis of character states in members of this major lineage. Their mutual arrangement was not solved. The clades IX and X (Amphialycus and Pachygnathus) are monophyletic. The group of the six remaining species in three clades (Lineage XI below) is problematic. It consists of ‘traditionally’ to the genus Alycus included species, and this time the characters are not good enough to solve, if the old genus is monophyletic or not. I chose not to divide it because another kind of classification, like establishing three new genera, would be worse and unfounded. ‘Character number/state’ refers to Table 2.

Lineage IX. Amphialycus. This minor group can be defined by eight progressive and one regressive states.

6/1. Presence of small lamellae subequal in size (Figs. 73, 84). Small lamellae have transformed subequal in size independently (see Lineage III, 3/1 and Lineage VI, 6/0 above).

12/1. Presence of pubescent setae on PS-segment (Figs. 72, 86). Elongated setae, along the way densely covered by cilia subequal in size, are typical to caudal segments and the prodorsal in-area (Fig. 71) of this group.

18/1. Presence of finely striated anterior pair of lateral eyes (Fig. 75). This regression might have appeared as a consequence of an adaptation to edaphic life. Lenses of other alycin lineages are glabrous (Figs. 12, 52).
33/1. **Presence of pubescent pair of setae in** (Fig. 71). The proximal pair of prodorsal setae is pubescent like the setae of the caudal segments, see 12/1 above.

35/1. **Presence of robust and elongated chelicera** (Figs. 4, 5). The elongation of chelicera has happened four times in Alycidae. Lineage V (Petralycini) has also preserved the robustness and a transformation to beak-like or stylet-like structures in Lineage X (*Pachygnathus*) and Lineage II (Bimichaeliinae), respectively, has happened.

40/1. **Presence of abaxially inserted pair of setae on chelicera** (Figs. 4, 5, 74). This is true for presently from Europe collected species, but there are two undescribed species ‘may’ and ‘clu’ in South Africa and one ‘amp’ in North America (probably Holarctic) with different cheliceral areas.

41/1. **Presence of well developed rutellum, with distal lobes** (Figs. 70, 74, 79). Unlike that of the other alycin lineages, the rutellum has a spoon-like, concave distal membrane.

52/1. **Presence of eupathids on tarsus I in high numbers.** The number of eupathids has also increased in Lineage V (Petralycini, Grandjean, 1943: 13, Fig. 8)

54/1. **Presence of densely setulated empodia** (Fig. 81). In contrast to the densely setulated empodia of *Amphialycus*, the sparse setulation in *Alycus* and *Pachygnathus* (Figs. 31, 65) can be considered to represent an early derived state.

**Lineage X. Pachygnathus.** This minor group can be defined by five progressive and two regressive states.

20/1. **Presence of a flap-like naso** (Figs. 52, 60). The naso may be like a broad flap also in *Amphialycus* (Fig. 71) and, in fact, the shape of naso varies a lot and independently in alycins. Naso bears an eye in the primitive state. Naso is grooved independently twice: it may be like a striated button as in *Amphialycus pentophthalmus* and a closely related undescribed species ‘pac’ from Polynesia or in Bimichaeliinae (cf. Figs. 4 vs. 100). Undescribed species with a deltoid naso have been found in South Africa, in North America and in Siberia or it may be lost but with the area still existing in *Alycus* (Fig. 25, counterparts of setae vi are far apart), and the whole area may even be missing as in the case of *oblongus* (Fig. 82). In most cases the alycin naso tends to be a proboscis whereas all petralycins have a pointer. So the variation is high in the Lineage Alycini compared to other tribes.

35/2, 37/1. **Presence of beak-like chelicera with a few minute teeth on outer edges of cheliceral chelae** (Figs. 3, 57, 63). Form and number of teeth may vary interspecifically but their presence on animals with predatory feeding habits is considered to be an early-derived character state. Reduction of dental size has connection to elongation and diminution of stalks and chelae of chelicera into beak-like apparatus of unknown feeding habits. See also Lineage IX, 35/1 above.

39/2. **Loss of cheliceral setae** (Fig. 3). Cheliceral setae are lost independently in Bimichaeliini and Petralycini. See also Lineage I, 39/1, 2 and Lineage IX, 40/1 above.

41/2. **Presence of small rutella, with tiny finger-like processes distally** (Figs. 58, 66). This reduction of rutella is obviously correlated with the diminution of chelicera (see above).

49/1, 50/1. **Presence of elongated trochanter IV and medially enlarged coxisternae II** (Fig. 7). Enlargement of the joint-sclerites of the coxal fields III and IV as well as enlarged trochanters IV (length ca. 50µm versus 30µm in *Alycus*) have led speculation to that these modifications might reflect an ability to jump (Kethley, 1990a).

**Lineage XI. Alycus.** This minor group can tentatively be defined by plesiomorphic states only. However, a definitive characterization should be left until examination of *A. marinus*.
from Europe, *A. selvaticus* from South America and an undescribed species ‘*agh*’ from South Africa by SEM.

12/6. **Presence of dorsal setae with basal ciliation and scaly shaft on PS-segment** *(Fig. 19, 26, 37, Alzuet & Delgado 1984: 89, Fig. 7).* The shaft is scaly on *A. roseus* and *A. denasutus* but the others seem to have the shafts more or less ciliated, and the shafts of the dorsal setae are also swollen on *A. marinus* *(Fig. 47).*

14/0, 19/1. **Absence of sclerotized crista and naso** *(Figs. 8, 25, 36, 47, Alzuet & Delgado 1984: 89, Fig. 7).* Basally narrow and slightly tapering naso, if present, is typical to most of the species examined. When naso is missing the nasal area still exists, i.e. the counterparts of setae *vi* are far from each other. Sclerotization on the cristal area may be prominent, only a narrow band, or absent, and the area covered by soft integument.

23/1, 33/1. **Presence of elongated pair of setae *vi* and pubescent setae in** *(Figs. 8, 25, 36, 47, Alzuet & Delgado 1984: 89, Fig. 7).* Primitively, the prodorsal setae are ciliated and more or less equal in size, but setae *vi, sce* and *in* may also be elongated and densely ciliated, whereas the setae *exp* are normally reduced in size.

29/0, 32/0. **Presence of prodorsal setae sce above anterior pair and pair of setae exp above posterior pair of the lateral eyes** *(Figs. 8, 25, 36, 47 and Alzuet & Delgado 1984: 89, Fig. 7).* Setae *sce* are always present and, primitively, the pair is above the anterior eyes but the position may also be removed anteriorly. The pair of setae *exp* is also always present (one exception: an Alycini species of unknown status from Tasmania, Prof. D.E. Walter, in. litt. The taxon is not included in the analysis.) and the smallest (less ciliated) pair on prodorsum. Position of *exp* is either above the anterior pair or, more primitively, above the reduced posterior pair of lateral eyes. Petralycins have lost the setae *exp*, and in holotrichous Bimichaeliinae (when the pair of *exp* is recognizable) the setae are equal in size to other prodorsal setae.

**A key to the European fauna.**

The solenidial numbers concern only the adult stages.

1. - Chelicerae beak-like, no cheliceral setae *(Fig. 3).*.... *Pachygnathus.*
   1a. - 6 pairs of prodorsal setae, setae *vi* on prodorsal shield *(Fig. 52), dorsal ridges slightly undulating*(Fig. 54), 2 solenidia on femur I *(Fig. 56).*.... *ornithorhynchus.*
   1b. - 7 pairs of prodorsal setae, setae *vi* on separate microshields *(Fig. 60), dorsal ridges strongly undulating*(Fig. 62), 5-7 solenidia on femur I *(Fig. 64).*.... *wasastjernae.*

- Chelicerae robust *(Figs. 2, 4, 5).*.... 2.

2. - Cheliceral shafts evenly tapering, elongated, one smooth cheliceral seta abaxially *(Figs. 4, 5).*.... 3. *Amphialycus.*
   3a. - Naso button-like *(Fig. 4), two solenidia on tarsus II, one solenidion on genu III.*.... *pentophthalus.*
   3b. - Naso flap-like *(Fig. 71), two solenidia on tarsus II, two solenidia on genu III.*.... *leucogaster.*
   3c. - Naso missing, setae *vi* very close to each other *(Fig. 82), one solenidion on tarsus II, no solenidia on genu III.*.... *oblongus.*

- Cheliceral shafts abruptly tapering, one or two pairs of cheliceral setae in dorsal position *(Fig. 2).*.... 4. *Alycus.*
   4a. - Naso narrow, curved, one pair of almost smooth cheliceral setae *(Fig. 13), 1 solenidion on tibia I, 1+0 solenidion on femur IV *(Fig. 11).*.... *roseus.*
   4b. - Naso missing, setae *vi* separated by median crista *(Fig. 25), one pair of almost smooth cheliceral setae *(Fig. 30), 1 solenidion on tibia I, no solenidion on femur IV *(Fig. 28).*.... *denasutus.*
   4c. - Naso narrow and curved downwards *(Fig. 36), two pairs of cheliceral setae, anterior one almost smooth, posterior one barbed *(Fig. 41), 2 solenidia on tibia I, 1+0 solenidion on femur IV.*.... *trichotus.*
   4d. - Naso flap-like *(Fig. 47), one pair of sparsely barbed cheliceral setae *(Fig. 48), 6 solenidia on tibia I *(Fig. 51), 3+1 solenidion on femur IV.*.... *marinus.*
4.4. *Alycus* C.L. Koch, 1842


*Pachygnathus s. str.* - Vitzthum, 1942: 797, not Dugès, 1834.

*Alycus* C.L. Koch, 1842 (s. st.)

Type species by monotypy *Alycus roseus* C.L. Koch, 1841 or 1842 (see *Remarks* 1) from Regensburg, southeastern Germany. No original material for this species has been preserved and the current concept of *A. roseus* is based on a detailed redescription by van der Hammen (1989). This redescription was based on material from Arnhem, The Netherlands, but it was also compared with toptypical material of *A. roseus* and topotypical material of *Pachygnathus dugesi* Grandjean, 1936 (Coulounieux, France).

Besides the type-species, *Alycus roseus denasutus* Grandjean, 1937 from France is raised to species status in this work. *Pachygnathus trichotus* Grandjean, 1937 from Algeria and *Pachygnathus marinus* Schuster, 1958 from France are listed here, although the latter only provisionally: the species has six sparsely ciliated palpal eupathids; sparsely ciliated empodia of the legs; and all the other characters mentioned below, but an examination of the fine morphology by SEM has not yet been possible. The genus has also been reported from South Africa, North America and South America; see *Unchecked* and *Remarks* (6).

The original description of *Alycus* is inadequate to allow its separation from present-day genera. The new delineation in Chapter 4.3., and more completely below, is based on fresh material collected all over Europe and examined by me using SEM. Although the illustrations of *A. roseus* by van der Hammen (1969, 1989) are
oversimplified, the description together with the description and figures of *P. dugesi* by Grandjean (1936, 1937a,b), are sufficient to stabilize the genus.

**Differential diagnosis.** The genus can easily be segregated from the other genera of the family by the robust and non-elongated chelicera (Fig. 2) and the three pairs of pseudacanthoid eupathids on palpi (Fig. 18).

**Description.** Medium-sized; soft integument with parallel ridges, sometimes shorter and more irregular on dorsal C-segment (Figs. 8, 9, 26, 37), transverse lamellae of various size-classes longitudinally aligned on ridges (Figs. 10, 27, 38), lamellae longitudinally on sclerotized integument (e.g. Figs. 8, 11, 25, 36); lenses of anterior pair of lateral eyes glabrous (Fig. 12); chelicera robust with non-elongated and glabrous shafts tapering to prominent jaws (Figs. 2, 13, 41, 48), a few teeth on cheliceral digits, mostly large in size (Figs. 2, 14, 30, 41, 48); well-developed rutella with a few large lobes ventrodistally (Figs. 16, 33, 44, 49); six eupathids on palpal tarsus apically (Figs. 18, 39, 50); combined coxisternae III-IV and trochanters IV not markedly enlarged (Fig. 6, ca. 30µm), empodia sparsely ciliated (Fig. 31).

**Unchecked published records.** Belgium, Lorraine, in André (1986: 114); Germany, in Vitzthum (1929); Schleswig-Holstein, in Alberti et al. (1981). Poland, Warsaw, in Niedbała et al. (1982). Argentina, Prov. de Buenos Aires, Reserva Natural e Integral de Punta Lara, 15 ex. as *Pachygnathus selvaticus*.

**Remarks 1.** In 1842 *Alycus roseus* was depicted by C.L. Koch in an outline drawing which, in fact, was intended as to demonstrate generic characters (Tab. IV, Fig. 22). This action, however, is sufficient to validate the genus and species according to Article 12.2.7. of the Code in ICZN (1999). The actual description of the species was published by C.L. Koch in DCMA (Vol. 37 nr. 19), which volume is, according to two external listings, published either in 1841 according to Oudemans (1936: 36) or in 1844 according to Sherborn (1923: 568). Rechecking of the contemporary literature should be done to confirm the correct dates for the often-cited "Hefte" of DCMA; the day of publication is not specified in any of the forty volumes of this work. In 1842 C.L. Koch gave a definition for *Alycus* which was no longer a monotypic genus but also included *Rhyncholophus devius* C.L. Koch, 1838 (see Chapter 8).

**Remarks 2.** The concept of *Alycus* has been quite differently interpreted by several specialists. Berlese (1887: A. M. S. fasc. 45 no. 5) used the name *Alycus roseus* and (1889a: A. M. S. fasc. 57 no. 10) the genus *Alicus* for the Italian species but he wrote *Pachygnathe velu* and *Pachygnathus*, respectively, in the beginning of his synonymy lists.

Berlese (1904) described *A. elongatus*, which is now in Nanorchestidae as *Speleorchestes e. * (see Castagnoli & Pegazzano, 1985: 126; Bernini et al., 1995: 32); *A. ornatus*, now in Lordalycidae as *Hybalicus o.* (see Berlese, 1913a: 78; Kethley, 1977: 61; Castagnoli & Pegazzano, 1985: 291); and *A. (Monalicus) arboriger*, now in Nanorchestidae as *Nanorchestes a.* (see Thor & Willmann, 1941: 147).

Berlese (1905) described *A. pyrigerus*, which now is in Pediculochelidae as *Paralytus p.* (see Castagnoli & Pegazzano, 1985: 346; Marshall et al., 1987: 28).

Berlese (1910a) described *A. (Monalicus) siculo*, now in Nanorchestidae as *Nanorchestes s.* (see Thor & Willmann, 1941: 148; Castagnoli & Pegazzano, 1985: 380),

Berlese (1916) synonymized *Sebaia palmata* Oudemans (1 Sept. 1904) with *A. (Monalychus) arboriger* Berlese (18 Aug. 1904).

Halbert (1920) described *A. latus*, which probably belongs to *Speleorchestes*, now in Nanorchestidae (see Thor & Willmann, 1941: 155) as *Leptalicus*.

**Remarks 3.** Kramer (1877), and later Womersley (1944), suggested that the genera *Pachygnathus* and *Alycus* might be separate. Grandjean (1936: 398) separated *Alycus roseus* from *Pachygnathus velu* and, according to him, both species could be any of his four new species. In Grandjean (1937a: 56) he still thought that they were separate, but either species could be identical to his *Pachygnathus dugesi*. Van der Hammen (1969) was of the opinion that *Alycus roseus* is not identical with *Pachygnathus villosus*.

**Remarks 4.** Oudemans (1903b, 1905) compared *Sebaia rosacea* and *Pachygnathus*, referring also to the figures of *Alycus roseus* by Berlese, see Remarks (2), and synonymized *A. and P.* in Oudemans (1931a). Oudemans (1937) listed many old references based on the supposed synonymy of *Alycus* and *Pachygnathus*.

### 4.4.1. *Alycus roseus* C.L. Koch, 1842

*Alycus roseus* C.L. Koch, 1842 vol. 3: 38, pl. 4 Fig. 22. - C.L. Koch, 1841 or 1844 Vol. 37 no. 19, Bavaria, Germany, Remarks (1); Walckenaer & Gervais, 1844: 194; 1847: 19, des Insectes Aptères pl. 38, Fig. 4, as *Alycus roseus*, copy from Fig. 22 by Koch (1842); Murray, 1877: 150, with a Fig. copied from Fig. 22 by Koch (1842); Kramer, 1882: 179, pl. 13 Figs. 1-4, ? not *P. r.* C.L. Koch, Unchecked and Remarks (5); Berlese, 1887: A. M. S. fasc. 45 no. 5, text and pl., Remarks (2, 7), not C.L. Koch; Frenzel, 1936: 30, Unchecked, Material; Grandjean, 1936: 398, Remarks (3); Grandjean, 1937a: 56, Remarks (3); Oudemans, 1937: 865, Remarks (4); Womersley, 1944: 133, 135, Remarks (3); van der Hammen, 1969: 177, Unchecked and Remarks (3); van der Hammen, 1970a: 3; van der Hammen, 1972: 12; Krantz, 1978: 229; Alberti *et al.*, 1981: 186, Figs. 15a, 15c; Walter, 1987: 277; Walter, 1988: 159, Unchecked and Remarks (6); van der Hammen, 1989: 127; Kethley, 1990a: 678; Kethley, 1990b: 1058, Unchecked and Remarks (6); Kethley, 1991: 130, Unchecked and Remarks (6); Norton & Kethley, 1994: 177; Uusitalo & Huhta, 1995: 333, Records; Walter & Proctor, 1999: 39; Alberti & Cooms, 1999: 548.


*Alycus roseus*. - Berlese, 1889: A. M. S. fasc. 57 no. 10, text and pl., erroneous orthography of *Alycus* C.L. Koch, Unchecked and Remarks (2, 7, 11), not C.L. Koch; Berlese, 1893: 34, 130, pl. 2 Fig. 6, pl. 4 Figs. 2, 3, 5, 7, 9, 11, Unchecked and Remarks (2, 7, 11), not C.L. Koch; Berlese, 1920: 78.

*Alichus rostratus* syn. nov. - Trägårdh, 1909: 11 nom. nud., unjustified emendation (or erroneous orthography) of *Alycus* C.L. Koch; Trägårdh, 1910: 466, Figs. 186-190, Records and Remarks (8, 9).

*Alichus rostratus*. - Trägårdh, 1910: 466, unjustified emendation (or erroneous orthography) of *Alycus* C.L. Koch; Thor, 1931: 231, synonymy list, Unchecked; Castagnoli and Pegazzano, 1985: 362, list of specimens at BA, Remarks (2, 7, 11); Banks, 1915: 20, Remarks (6); Hull, 1918: 36, Unchecked.


**Pachygnathus roseus** (Koch). - Grandjean, 1942: 89 (= dugesi Grandj.); Bottazzi, 1950b: 387, Unchecked and Remarks (7, 11); Schweizer, 1951: 56, not C.L. Koch, Records sub Amphialycus leucogaster and Remarks (20); Bottazzi, 1951: 225, Unchecked and Remarks (7); Krivolotisky et al., 1978: 93, Figs. 300a, b and v from van der Hammen (1969), 300g original?.

**Alycus ? roseus**. - Womersley, 1944: 139 Figs. 3F-I, not A. r. C.L. Koch, Material, Unchecked and Remarks (25).


**Pachynatus sp.** - Livshitz & Mitrofanov, 1975: 82, 159, Fig. 77A-Z; Kranz, 1978: 312, Figs. 57-1, 57-3, Unchecked; Heyer & Ryke, 1966: 333, Unchecked; Loots & Ryke, 1966: 183, Unchecked.

**Alycus roseus** Grandj. - Vainshtein, 1977: 13, Fig. 2 from van der Hammen (1969), erroneous author.

**Pachygnathus nr dugesi** Grandjean. Kamill et al., 1985: 278, Unchecked and Remarks (6).

A holotype has not been designated. Especially the illustration by van der Hammen (1969) is oversimplified but the description and figures by Grandjean (1937a, b) of the junior synonymy *Pachygnathus dugesi* are diagnostic enough to identify the species. There is, however, a potential neotype from totopotypic material, Germany, Regensburg on a slide with three labels: "Pachygnathus villosus Dug. (dugesi Grdj.)", "bei Regensburg. leg. Sellnick", "Det. C. Willmann". The potential neotype is marked by a red ring. Another specimen is in lateral position on the same slide, which is deposited at ZSS, München, Germany.

**Differential diagnosis.** This reddish species can be separated from the other species by dorsal integument with short, irregularly arranged ridges (Figs. 8-10); long, narrow, and strongly downwards bent naso (Fig. 8); one pair of smooth cheliceral setae (Fig. 13); and rutella with an apical point and three ventrodistal lobes (Figs. 16-17).

**Description.** Length 350-560μm (Fig. 9); colour reddish/violet in alcohol; dorsum, venter and legs infected by neotrichy, ciliate dorsal setae with a long central point (Figs. 8-10, 19-23); on prodorsum: setae exp above reduced (lensless) pair of posterior eye areas, narrow strip of hard integument continuous from proboscis-like naso up to sensillar area covered by longitudinal lamellae of various size classes (Figs. 8, 12); one smooth cheliceral seta (sometimes with a barb or two) dorsally on chelicerae (Figs. 13-15); rutella with three ventrodistal jutting projections and an apical point, above which usually a small protrusion, three pairs of adoral setae (Figs. 16-17); six eupathids with long cilia on palps apically (Fig. 18); genital setae 18-24 per valve; anal setae 6-7 per valve; solenodial formula for tarsi, tibiae, genua and femora on legs I-II-III-IV, respectively, as given below, solenidion o2 at the adaxial end of lyrifissure on tarsi I, 01 present on femora IV (Fig. 11), famulus II forked (Fig. 24).

All instars have a cleavage line of prodehiscent type (see Norton & Kethley, 1994).

**Larva** (n=1, Fig. 152)
- length 175 μm
- dorsal holotrichy
- sensilla slightly swollen
- two pairs of adorals
- no genital opening
- three pairs of legs
- empodia clawless
Protonymph (n=1)
- length 185 μm
- slight neotrichy
- sensilla slightly swollen
- one pair of genital setae
- empodia on leg IV clawless

Deutonymph (n=1)
- length 250 μm
- 4-7 genital setae per flap

Tritonymph (n=1)
- length 350 μm
- 9-14 genital setae per flap

Adult female (n=several)
- length 350 μm or more
- no cleavage line
- 18-24 genital setae per flap
- one pair of eugenital setae

Adult male (n=several)
- length 350 μm or more
- no cleavage line
- 18-24 genital setae per flap
- ten pairs of eugenital setae

Alycus roseus is widely distributed in Europe and possibly Holarctic. In terms of natural forest habitats the species is almost ubiquitous. It seems to live in a wide variety of litters of European trees and bushes, as well as in mosses.


Germany, bei Regensburg, MS: 2 ex. on slide as *Pachygnathus villosus* Dug. (*dugesi* Grdj.), Det. C. Willmann, at ZSS. The toptype (potential neotype) marked by red ring.


Norway, Oslo, Bygdøy, Kungsparken, 60°N 11°I, moss on *Myrtillus*-type forest, 15 Sept. 1993, MU: 1 ex., U37; Finse, Hardangervidda, 60°N 8°I, moss and hay close to glacier Bloisen, 1220 m, 12 Sept. 1993, MU: 2 ex., U42.

Poland, Krynica, 49°50'N 21°E, rotten *Picea* and moss, 1 Sept. 1992, MU: 5 ex., U237, U267.

Sweden, probably Sarek, 1903, IT: 1 ex. as *Alichus rostratus* at NRM,

**Remarks (8).**

Russia, Tuva Republic, SE-shore of lake Tere-Khol', 1150 m, 50°01'N 95°03'E, LH *Ribes, Betula* and *Populus laurifolia*, 12 June 1995, MU: 3 ex., U308; Tuva Republic, S-range of Tannu Ola, 1500 m, 50°'47"N 94°21'E, LH *Larix, Caragana, Verbascum, Viola, Ranunculus, Galium* and *Thuidium*, 8 June 1995, MU: 6 ex., U311.

**Unchecked published records.** Austria, Granatspitzgruppe, Stubachtal, *Sphagnum*, 1600 m, in Franz (1943) as *Pachygnathus villosus*.

Denmark, Jaegersborg Dyrehave, in Haarløv (1957) as *Pachygnathus villosus*;

France, in Grandjean (1937a) as *Pachygnathus dugesi*.

Germany, Thüringer Wald, Spruce forest, in Kramer (1882), Remarks (5);

Germany, Göhrbersdorf, Wiesenboden, in Frenzel (1936), Material.

Italy, Padova, in G. Canestrini & Fanzago (1877); Portici, Firenze, Pisa, Roma, Chianti, Mugello, on several slides and 1 vial as *A. roseus* at BA acc. Castagnoli & Pegazzano (1985), see Remarks (11, 12); Prato Spilli, 1700 m, Apennines of Parma and Casera Moraret, 1600 m, Alpi Carniche, in Bottazzi (1950b) as *Pachygnathus roseus*; Casera Moraret, 1800 m, *Larix* detritus, in Bottazzi (1951).

The Netherlands, Arnhem, garden litter of *Taxus baccata*, in van der Hammen (1969) 25 ex..

Norway, central and southern parts, in Thor (1931) not rare.

UK, West Allendale, in Hull (1918).

Republic of South Africa, soil under *Acacia karroo*, in Meyer & Ryke (1966) cf. Theron (1979); RSA, pasture soils, in Loots & Ryke (1966) 3851 ex., cf. Theron (1979); RSA, Theron (1979) several spp. in several genera, will be published in another context. I have seen a small sample of slides, for comparison.

Canada, Quebec, woodland humus, in Marshall & Kevan (1964).

Remarks 5. The status of material identified as *Alycus roseus* by Kramer (1882) from Germany is uncertain. The description and figures of light violet integument, *in*-setae longer than the dorsal setae, without naso, and without cheliceral setae do not quite correspond to the present definition of the species, but this may be a question of inaccuracy in observation and drawing techniques.

Remarks 6. Banks (1904, 1915) wrote that *A. r.* probably has not yet been found in US and Krantz (1978) still presented *A. r.* as a European species but now both Walter (1988) and Kethley (1990b, 1991) have reported it from six states in USA (see Unchecked). Kamill *et al.* (1985) used both *Pachygnathus dugesi* and *P. nr dugesi* for specimens from New Mexico. A solitary specimen from the OSU Collection examined by me differs from the European species in some respects. More material should be checked to judge the value of differences in terms of a new morphospecies.

Remarks 7. According to Bottazzi (1950a: 32) there are representatives of two species among the specimens identified by Berlese as *Alycus roseus* C.L. Koch, and she described *Pachygnathus berlesei* from the material, Remarks (12). The other species Bottazzi (1950b) described as *Pachygnathus lombardinii*, while she also reported *Alycus roseus* C.L. Koch (as *Pachygnathus roseus*) from Italy, Remarks (11). I have not examined the material identified as *Alycus roseus* at BA or in Parma (Unchecked) and it remains open, whether any of the specimens in the collections belong to Koch’s species (Material). In any case, all the figures by Berlese are referable to *Alycus trichotus*.

Remarks 8. The specimen of *A. rostratus* in the Trägårdh Collection (NRM, Stockholm) was examined by me using a phase-contrast microscope. The *Alichus*-slide is from the remounted ones with the original label "No. 8. 03 I. T-dh", in Trägårdh's handwriting, firmly attached to it. It probably means Sarek, 1903 (I. Trägårdh), but "No. 8" is not the same numbering as in his 1910 Sarek paper (Curator T. Kronestedt, in litt.).

Remarks 9. Although Thor (1931: 231) wrote “*?Alichus rostratus*” (i.e. with a question mark) on his synonymy list of *A. roseus* on the basis of Trägårdh's description, he later (Thor & Willmann 1941: 138) accepted *P. rostratus* as a good species. Therefore this synonymy is presented here as new.

4.4.2. *Alycus denasutus* (Grandjean, 1937) comb. and stat. nov.

*Pachygnathus dugesi* ssp. *denasutus*. - Grandjean, 1936: 398, comparisons between non-specific characters; Grandjean, 1937c: 199, Fig. 6A-C, Strasbourg, France, Unchecked and Remarks (10).


*Alycus roseus* *denasutus*. - van der Hammen, 1969: 193, Material and Remarks (10).

(Figs. 2, 25-35)

A holotype has not been designated, see Material.

Differential diagnosis. This species is closely related to *A. roseus* but the colour is white, winding ridges are long and parallel on dorsum (Figs. 26-27) and the naso is missing (Fig. 25).

Description. Length 350-500 μm (Fig. 26); colour white in alcohol; parallel ridges on soft integument winding, mostly continuous (Figs. 25-27); on prodorsum: naso missing, strip of hard integument between nasal area and sensillar area interrupted by ridges of soft integument, distance between counterparts of setae *in* and sensilla *ve* subequal to distance between counterparts of setae *vi* (Fig. 25); chelicera with one pair of setae dorsally (Figs. 2, 29-30); rutella with a broad shaft with or without a finger, with three ventrodistal projections, and an apical point with or without a small protrusion
dorsobasally (Figs. 33-35), three pairs of adoral setae; palpi with three pairs of eupathids; genital setae 15-20 per valve; anal setae 6-7 per valve; solenidial formula as given below, solenidion 01 missing on femora IV (Fig. 28), tiny barbs on famulus II (Fig. 32).

*Alycus denasutus* has been collected from coniferous and deciduous forests and the species is possibly Holarctic, but rarer than *A. roseus*.


USA, South Carolina, Beaufort Co., Hilton Head isl., *Sea Pines*, ex litter back dunes, brushy area, AM, 15 August 1997 VE LaRoche: 1 ex., OSUAL0000122.

**Unchecked published records.** France, Strasbourg, in Grandjean (1937c) 5 ex., Remarks (10).

**Remarks 10.** Grandjean (1937c: 199) described *Pachygnathus dugesi* *denasutus* from Strasbourg, France. Van der Hammen (1969: 193) proposed two other subspecies based on differences in rutellar structure and in chaetotaxy of legs. He found Dutch specimens of *A. roseus* with bases of rutella broad like in *denasutus* (Figs. 16 and 34) and three setae (instead of two) on telofemora IV, compared to the setal formula reported by Grandjean from Dordogne, France. New observations indicate that rutella of the *denasutus*-type also may or may not have a finger-like process ventrally (Figs. 33-34), and the specimens belong to the same Italian population, whereas an American specimen has tiny dorsal projection in base of pointer like on *A. roseus* (Figs. 35 and 16). Obviously variation in the structure of rutella is not geographically restricted but rather a stochastic phenomenon. Also a one-seta-difference in chaetotaxy lies within the limits of normal intraspecific variation in these neotrichous species. Grandjean, on the other hand, established the subspecies *denasutus* when differences between the species were regarded to be more pronounced (now e.g. *P. villosus* vs. *P. wasasjernae*, or *B. augustana* vs. *B. sarekensis*, see Appendix 2), other nasoless species were not known (now *Amphialycus oblongus*, an undescribed species sub *Pachygnathus* sp. in Krantz (1978: 312, fig. 57-1; an undescribed species ‘nas’ in South Africa) and when the known distribution of *A. denasutus* was limited to Strasbourg (now four more localities in Italy and USA). Also, in addition to differences in colour, nasal area, rutellar shaft and solenidial formula, listed by Grandjean (1937c), the examined specimens differ from *A. roseus* at least in the pattern of dorsal ridges and structure of famulus II (Figs. 10 vs. 27 and 24 vs. 32). The new status of *A. denasutus* as a morphospecies seemed to be justified, but the division of *A. roseus* into subspecies is unfounded.

**4.4.3. Alycus trichotus** (Grandjean, 1937) comb. nov.

*Pachygnathus trichotus.* - Grandjean, 1936: 398, comparisons between non-specific characters; Grandjean, 1937c: 200, Fig. 7A-F, type species by original designation from Algeria, Unchecked and Remarks (11); Thor & Willmann, 1941: 139, Fig. 193a-e acc. Grandjean, description; Mihelčič, 1958: 277 from Spain, Records and Remarks (13); Krivolutsky et al., 1978: 96, Fig. 302a-e after Grandjean, 1937c.

*Alycus roseus.* - Berlese, 1887: A. M. S. vol. 45. no. 5, Figs. 1-8, not C.L. Koch, Unchecked and Remarks (11).

*Alicus.* - Berlese, 1889a: A. M. S. vol. 57 no. 10, Figs. 1-6, misspelling, not C.L. Koch.
Alicus roseus. - Berlese, 1893: 34, pl. 2 Fig. 6, pl. 4 Figs. 2, 3, 5, 7, 9, 11, misspelling, not C.L. Koch.

Pachygnathus berlesei syn. nov. - Bottazzi, 1950a: 32, Figs. 1-6, Unchecked and Remarks (11, 12); Bernini et al., 1995: 32.

Pachygnathus lombardini syn. nov. - Bottazzi, 1950b: 389, Figs. I, II/1-2, III/1-3, Unchecked and Remarks (11) and Material; Bernini et al., 1995: 32.

A holotype has not been designated, see Material. The species is transferred to Alycus because of transverse lamellae of various size, non-elongated chelicera and three pairs of palpal eupathids with a reduced number of barbs (which character states, however, are considered as plesiomorphisms by earlier authors).

Differential diagnosis. This species can easily be segregated from other alycins by its high neotrichy on dorsum, pubescent dorsal setae (Figs. 36-38), two pairs of setae on chelicera (Fig. 41), long cillum of a palpal eupathid (Fig. 39), and a forked pair of adoral setae (Fig. 46).

Description. Length 350-550 μm (Fig. 37); eight (instead of nine) hysterosomal segments; prominent neotrichy on dorsum by pubescent setae (Fig. 37); on prodorsum: pubescent pair of setae in ca. twice in length beside setae on C-segment, setae see and exp close to each other anteromedially to eye lenses, ciliate setae vi ca. three times longer than setae on C-segment, naso conical, bothridia of posterior sensilla sci bent (Fig. 36); chelicera with pattern of short ribs, cheliceral shafts short and stout with two setae dorsally: anterior one with a few tiny barbs if any, posterior one with a few distinct barbs on upper side (Figs. 41-43); rutella with four distal lobes and either with or without a small pointer (Figs. 44-45); two pairs of adoral setae, abaxial being forked (Fig. 46), additional setae on subcapitulum; palpal tarsi with six eupathids: five of them pseudacanthoid but adaxial one of the median pair with a long and bent cillum, abaxial one nude (Fig. 39); genital setae 18-24 per valve (Fig. 6); anal setae 6-12 per valve; solenidial formula as given below, o2 on tarsi I slightly anterior to adaxial end of lyrifissure.

Alycus trichotus has only been found in rotten vegetation on limestone rock in the Mediterranean area.

Records. Italy, Venice, exhibition area, leaf litter, 2 August 1984 MU: 5 ex. on stub U357 at ZMT; Siena, Porta San Marco, LH alongside the city wall under Robinia, Avena, 26 July 2000 MU: 5 ex. on U356, 5 ex. on U358 at ZMT.

Spain, Madrid, Valdemoro, 16 May 1954 WS: 2 ex. as Pachygnathus trichotus on slide no.20.02/7559 at the Mihelčič Collection, MNCN, Remarks (13); no place, no date, no collector: 1 ex. as Pachygnathus trichotus on slide no. 20.02/7639 at the Mihelčič Collection , MNCN.

Unchecked published records. Italy, AB: probably several ex. as A. roseus in Castagnoli & Pegazzano (1985) at BA; Florence, Pisa, Parma, in Bottazzi (1950a) as Pachygnathus berlesei, Remarks (7, 11, 12); Apennines near Parma, Monte Penna, 1600 m, Padova, beech litter, in Bottazzi (1950b) as Pachygnathus lombardini, Remarks (11).

Algeria, county of Constantine, Hammam Meskoutine, in Grandjean (1937c) 4 females and 1 deutonymph, as Pachygnathus trichotus, Remarks (11).

Remarks 11. Grandjean (1937c) proposed Alycus roseus sensu Berlese (1887) to be conspecific with A. trichotus, whereas Bottazzi (1950a, 1950b) considered Berlese's specimens, identified as Alycus roseus, to be a collection of two species. She
described two new species of alycins, *P. berlesei* and *P. lombardinii*, both with setae *vi* longer than setae *in* (Fig. 36), two pairs of cheliceral setae (proximal being barbed) (Fig. 41), three teeth on cheliceral fixed digits (inner surface in Fig. 41) and distally lobed rutella without an apical point (Fig. 45), as in *P. trichotus*.

Bottazzi (1950a: 32) was aware of the description of *P. trichotus* by Grandjean (1937c) and all the diagnostic characters listed above when she prepared a key to the alycins known up to then (Bottazzi, 1950b: 392). She did not give any counterpart for specific characters, like exceptionally dense neotrichy (Fig. 37) which also is evident from Berlese's illustration, forked adorals (Fig. 46), body of eight segments (Fig. 37), and solenidial formula, either for *P. berlesei* or for *P. lombardinii*, although she commented (Bottazzi 1950b: 390) that, exclusive of the character states listed below, the species was otherwise similar to *P trichotus*. Instead, the characters she used to separate her species from *P. trichotus* and in the key are either continuous or vulnerable to variation in preparation process, i.e. tenuous characters varying intraspecifically for natural and artificial reasons.

1. **Body length** for *P. berlesei* (335 μm) is based on a male (Bottazzi 1950a: 34, Fig. 6, male eugenitals) and the length for *P. lombardinii* (540 μm) on a female (Bottazzi 1950b: 390, Fig. III/3, female eugenitals): this may still be in limits of the intraspecific variation which is high on these soft-bodied mites in which males are usually smaller (e.g. Grandjean 1937c: 199; 1937d: 262).

2. The measurable **length of sensilla** depend on the angle they happened to have been settled down during the slide making process and the extremely thin distal ends of sensilla can easily be lost or neglected. On the Spanish specimens examined by me (Records) the anterior pair of sensilla was longer than the posterior pair, as for *P. berlesei sensu* Bottazzi (1950a: 33, Fig. 1), but for *P. lombardinii*, both pairs were subequal in length in the Figure I by Bottazzi (1950b) as well as the sensilla in the figure 7A by Grandjean (1937c) for *trichotus*.

3. All the setae on **palpal tarsi** are similarly barbed (Bottazzi 1950a: 34, Fig. 3, *berlesei*; 1950b: 390, Fig. II/1, *lombardinii*) besides which she missed the palpal solenidion: palpi without any transformed seta, i.e. apical eupathids or a solenidion, simply do not exist in this family.

4. Most specimens of *A. trichotus* from both Spanish and Italian populations have some tiny barbs on the upper surface of **anterior cheliceral setae** (Figs. 42-43, and Fig. III/1 in Bottazzi 1950b: 390, for *lombardinii*), while Bottazzi (1950a: 34, Fig. 2, for *berlesei*) and Grandjean (1937c: 201, Fig. 7c, for *trichotus*) did not report barbs in the specimens they examined and described, and the chelicera resemble that in Figure 41. Sometimes I have also observed barbs near the base of the "smooth" cheliceral seta of *A. roseus* (Figs. 13, 15). The presence or absence of barbs is obviously a matter of intraspecific variation.

5. In the well macerated specimens of *A. trichotus* from Spain, pigment has been totally lost and **eye spots** are difficult to locate, but at least the reduced posterior pair always exists in the alycins, and also this pair is missing in the Figure I by Bottazzi (1950b: 388, for *lombardinii*). In fact the anterior eye lenses also seemed to be missing in Figure I by Bottazzi (1950a: 33, for *berlesei*), because the anterior pair should be in line with the posterior sensilla rather than being inserted next to shoulders as the black spots in the figure, which spots therefore rather symbolize the reduced posterior pair of lateral eyes.

In conclusion, the supposed loss of both palpal eupathids and eye spots seemed to be based on inadequate observation, whereas the body length, relative lengths of sensilla and number of barbs on cheliceral setae vary in specimens of *A. trichotus* from
Algeria, Spain and Italy and no specific character state for either *P. lombardinii* or *P. berlesei* can be indicated. Therefore the two species described by Bottazzi are here considered to be junior synonyms of *A. trichotus*.

**Remarks 12.** Bottazzi visited BA and examined e.g. vial 36°/1754 from Mugello, on which she probably based her description of *P. berlesei* (Dr. R. Nannelli, pers. comm.), Remarks (7).

**Remarks 13.** Detailed information of the sampling is missing on labels at the Mihelčič Collection, MNCN in Madrid. Mihelčič (1958: 269, 277) gives locality and habitat for *P. trichotus* as follows: Ciempozuelos (limestone soil) ca. 40 km S from Madrid in litter of *Quercus ilex*. Slide no. 20.02/7559 is with the note: T 82, and in addition there are 6 ex. oribatids; slide no. 20.02/7639 is with the note: Mí 173, there are also 4 ex. as *Smaris squamosa*, 1 ex. trombidid, 1 ex. eupodoid.

*Pachygnathus* sp. on the labels of three other slides is based on misidentifications. Instead, there are: slide no. 20.02/7482 with 1 ex. as *Bdella semiscutata*, 1 ex. bryobid L, 1 ex. penthaleid; slide 20.02/7483 with 1 ex. as *Penthalodes major*, 5 ex. as *Zercon vacuus*, 1 ex. bryobid, 1 ex. anystid; and slide 20.02/8120 with 1 ex. as *Ologamasus calcaratus*, 1 ex. penthaleid.

**4.4.4. Alycus marinus** (Schuster, 1958) comb. nov.

Trombidiformes. - Schuster, 1956: 244.


(Figs. 47-51, Fig. 48 after Schuster, 1958)

Holotype from France, Riou Island near Marseille at SMF was examined by me using a phase-contrast microscope. Specimens should be examined by SEM. Even if the species is not a nematode-feeder, it is provisionally included in *Alycus* because of the robust and non-elongated chelicera, sparsely barbed palpal eupathids, sparse ciliation of empodia and lobed rutella with a pointer.

**Differential diagnosis.** This species can be segregated from other species by its swollen and pubescent dorsal setae (Fig. 47), one pair of sparsely barbed cheliceral setae (Fig. 48), and a missing anterior pair of eye lenses (Figs. 47, Remarks 14).

**Description.** Length 450 µm; hysterosomal segments marked by rows of swollen and pubescent setae (Fig. 47, Remarks 14); ventral setae densely ciliate; on prodorsum: anterior pair of lateral eye lenses missing, swollen and pubescent setae *sce* and *exp* inserted anterior to a reduced pair of lateral eyes, flap-like naso bent downwards, densely ciliate setae *vi* exceptionally long, slightly swollen at the base, sensilla *sci* and *ve* ciliate all their length, swollen and pubescent setae *in* slightly smaller in size than the setae on C-segment (Fig. 47, Remarks 14); cheliceral shafts with one prominent tooth, one dorsal cheliceral seta distinctly but sparsely barbed on upper side (Fig. 48, Remarks 14); pointed rutella with broad ventral extension, three pairs of adoral setae, additional setae on subcapitulum (Fig. 49); six sparsely barbed eupathids of pseudacanthoid type on palpal tarsi (Fig. 50); genital setae 14-16 per valve; anal setae 8-11 per valve; maximum number of solenidia observed in solenidial formula as given below, ω2 on tarsi I anterior to adaxial end of lyrifissure, two baculiforms on tibiae I (Fig. 51, Remarks 14).

So far *Alycus marinus* is reported only from the Mediterranean littoral environment in France.
Records. France, Riou Island, near Marseille, RS: Holotype, access no. 17136 at SMF; France, RS: 6 ex. as ?Pachygnathus on two slides at the Willmann Collection, ZSS. On both slides only a note by Willmann: “11 M Schuster”, but see above.

Remarks 14. In comparison to Schuster’s description (1958, Figs. 8-10): (1) The posterior pair of lateral eyes also is indicated in his Fig. 8, although he writes: "fehlende Augen und Augenhöcker"; (2) Concerning the comment: "ohne segmentale Hysterosomal einschnürrungen", in swollen specimens there are still seta-free zones between setal rows to mark limits of segments (Fig. 47); (3) Sensilla in Fig. 8 are smooth proximally but the whole length of sensilla is barbed in the specimens from the Willmann Collection; (4) The unfavourable position of chelicera in all the six specimens examined by me did not allow proper drawing of teeth and digits, but insertion of the cheliceral seta far behind the bases of digits suggests that the missing seta might be the anterior one (Fig. 48); (5) Dehiscence line (Fig. 47) also is present in the illustration of prodorsum by Schuster (Fig. 8). It might suggest that if his solenidial counts also included non-gravid specimens, then some lower numbers of the high variation reported by him might originate from tritonymphs with a pair of eugenital setae as well.

The observed number of solenidia in the European Alycus on legs I-II-III-IV:

<table>
<thead>
<tr>
<th></th>
<th>tarsi</th>
<th>tibiae</th>
<th>genua</th>
<th>femora</th>
</tr>
</thead>
<tbody>
<tr>
<td>roseus</td>
<td>2-1-0-0</td>
<td>1-2-2-0</td>
<td>4-2-2-1</td>
<td>2-0-0-1</td>
</tr>
<tr>
<td>denasutus</td>
<td>2-1-0-0</td>
<td>1-2-2-0</td>
<td>4-2-2-1</td>
<td>2-0-0-0</td>
</tr>
<tr>
<td>trichotus</td>
<td>2-1-0-0</td>
<td>2-2-2-0</td>
<td>3-2-2-2</td>
<td>3-0-0-1</td>
</tr>
<tr>
<td>marinus</td>
<td>2-1-0-0</td>
<td>6-4-4-1</td>
<td>6-2-3-2</td>
<td>4-1-0-3+1</td>
</tr>
</tbody>
</table>

4.5. Pachygnathus Dugès, 1834 (s.st.)

Pachygnathus Dugès, 1834b: 54, pl. 8, Figs. 52-55, type species by monotypy Pachygnathe velu from France. - Méneville, 1836: 112, reference to Dugès; Oken, 1836: col. 518, P. villosus, brief diagnosis and reference to Figures by Dugès; Cuvier & Voigt, 1836: 425; Burmeister, 1837: 579; Milne Edwards, 1838, 2nd ed. vol. 5: 59 (Pachygnathe), 84, diagnosis by Dugès; 1838 3rd ed. vol. 2: 284, 293, not seen; 1845, 2nd ed. register vol. 11: 576, not seen; Lucas, 1840: 470, diagnosis by Dugès; 1847: pt. 36 Fig.8, copy from Fig. 52 by Dugès; Murray, 1877: 117, 127, brief diagnosis, 128, a Fig. copied from Fig. 52 by Dugès; Kramer, 1877: 222, 234, definition of subfamily Pachygnathidae (fam. Prostigmata) for Pachygnathus; Grandjean, 1936: 398; 1937a: 56; 1937b: 134; 1937c: 199; 1937d: 262, in part (P. ornithorhynchus only); Grandjean, 1937c: 202, P. ornithorhynchus, Remarks (16); Walter, 1988: 159, not Dugès, 1834b, Remarks (15); Kethley, 1990a: 678, Remarks (15); Lindquist & Palacios-Vargas, 1991: 360; Norton et al., 1993: 44.

Pachygnathus s. str.: Vitzthum, 1942: 797, not Dugès, 1834, syn. Alycus, C.L. Koch.

Alycus. - Jesionowska, 1996: 329, reference to Fig. 6 as A. ornithorhynchus.

Dugès (1834b: 54, pl. 8, Figs. 52-55) established the genus Pachygnathus for a reddish, hairy mite with large eyes, linear palps, chelate chelicera with thick basis, suture between prodorsum and dorsum, legs in two groups, first pair of legs strongest and longest (and then IV, III and II, respectively), the femora being thickest and tarsi the longest segments, with two large claws. Unfortunately, he only used the French vernacular name Pachygnathe velu of the species which is not in accordance with the International Code of Zoological Nomenclature. Oken (1836, col. 518) listed the only species in this genus as
Pachygnathus villosus without author name and without direct reference to velu, but referring to the numbers of figures of velu by Dugès (1934b).

No original material of the type species has been preserved and the original description of type species (by monotypy) Pachygnathe velu Dugès, 1834 (Pachygnathus villosus Dugès [in Oken], 1836) from France is too superficial, partly misleading, and is insufficient to show features used to separate present-day genera. Therefore several species by authors have been interpreted to be junior subjective synonyms to the species.

Firstly, the general habitus (Fig. 52) fits any known European member of Alycidae, but the details are confusing, poor or plainly wrong, most probably based on difficulties of observation with the optical equipment of that time available to Dugès:

1. Empodia are missing (Fig. 55), but actually always present in all alternative genera (Figs. 31, 65, 81, 99, 150).

2. Straight hairs on tarsus I plus loss of third claw (Fig. 55) would fit to Bimichaelinæa (Fig. 91), while presence of eyes (Fig. 52) and thick chelicera (Fig. 54) do not; the abundance of curved hairs on hysterosoma (Fig. 52) could probably fit to Laminamichaelia setigera (Fig. 121), or simply is artificial of origin, due to inappropriate mounting.

3. Approximate form of chelicera, loss of cheliceral setae (Fig. 54) and two stiff apical hairs on palpal tarsi (Fig. 53) are as in Petralycus (Figs. 143, 145), but the presence of eyes and the general neotrichy (Fig. 52) do not fit.

4. The eyes and cheliceral structure in general have their counterparts in Alycus (Fig. 8), but these species are not edentate (Figs. 13 vs. 54), have cheliceral seta (Figs. 13 vs. 54), and three tarsal claws (Figs. 31 vs. 55).

5. Pachygnathus has the tarsi not bidactyl, but tridactyl (Figs. 65 vs. 55), and cheliceral shafts, although thick in basis, are much thinner and more elongated (Figs. 3 vs. 54).

6. Setal formula of palpi, based on Fig. 53 of Dugès, is:
0-2-2-2-(2+5) for villosus. Grandjean (1937a, c, 1943) gives:
0-2-1-3-12 for P. ornithorhynchus;
0-2-1-3-13 for P. dugesi (= A. roseus);
0-2-1-2-9 for P. unicornis;
0-2-2-3-12 for B. diadema (= L. setigera).
The form and numbers of setae on tarsus I (Fig. 55) and palpus (Fig. 53) in the detailed figures of Dugès (1834b), might be exactly what he saw, and again, do not fit.

Although the original description of the Pachygnathe velu (Pachygnathus villosus) does not completely fit any known species of Alycidae, the name Pachygnathus has been extensively used. Judson (2000) notes that the identity of P. villosus should be fixed by the designation of a neotype to finally resolve the separation of Pachygnathus and Alycus. Fixing of the type species of the genus to an identifiable species with type material would be less confusing than suppression of this generic name.

A feasible way to solve the problem would be to make Pachygnathus villosus an objective synonym with a recognizable species Pachygnathus ornithorhynchus, well described by Grandjean (1937c). Both Pachygnathus and Alycus are used in current literature (Kethley, 1990a: 676, 678; Lindquist & Palacios-Vargas, 1991: 360; Norton et al., 1993: 23, 44). Then the other old generic name Alycus of this family could also be regarded as permanently fixed.

The structure of mouthparts of Pachygnathus s.s.t. suggests a feeding behaviour which profoundly differs from that of Alycus and well justify separation of the species with beak-like chelicera into their own genus (Remarks 15). Kethley (1990a: 675)
discussed the possible saltatorial modifications in *Pachygnathus* as a result of the enlargement of the fourth pair of legs.

In the absence of material appropriate for the neotype designation, however, in this work only the subjective synonymy of *Pachygnathus ornithorhynchus* Grandjean, 1937 with *Pachygnathus villosus* Dugès *in Oken*, 1836 is accepted. The new character states of the genus in Section 4.3 and, more completely, below is based on knowledge of two species from Europe and one undescribed species ‘olo’ from Polynesia. An undescribed species ‘nas’ from Africa belongs also here.

**Differential diagnosis.** The genus can easily be segregated from the other genera of the family by the beak-like chelicera (Fig. 3), small, fork-like rutella (Fig. 58) and less than six sparsely barbed eupathids on palpi (Fig. 63).

**Description.** Soft integument with gently undulating ridges, transverse lamellae longitudinally aligned on ridges, their size increasing up the ridges, being largest at ridgetops and smallest between ridges (Figs. 54, 62), sclerotized integument with short striae (Figs. 52, 56, 60, 64); anterior eye lenses smooth, naso a broad and long flap (Figs. 52, 60); cheliceral shafts tapering abruptly into distal beaks (Fig. 3), teeth of cheliceral digits few and minute, but obvious in SEM (Figs. 57, 63); reduced rutella with minute lobes distally (Figs. 58, 66); four to five palpal eupathids with a few barbs basally (Figs. 55, 63); combined coxisternae III and IV strongly enlarged medially (Fig. 7), trochanters IV elongated (Fig. 7, ca. 50 μm), empodia sparsely ciliated (Fig. 65).

**Remarks. 15.** Walter (1988: 159) proposed some species of *Pachygnathus* to be predators of soft-bodied microinvertebrates, but on the next page he referred to the feeding habits of *Pachygnathus marinus*, which differs from the species of the present definition of *Pachygnathus* by cheliceral structure, and is now transferred to the genus *Alycus*. Perhaps Kethley (1990a: 678) also had this difference in mind when he understood the genus *Pachygnathus* as an assemblage of species groups. Also in his concept (p. 678), one species of *Pachygnathus* in the *P. ornithorhynchus* group is thought to be a predator of copepods and tardigrades, referring to Schuster (1979), who reported *Pachygnathus marinus* with massive chelicera.

### 4.5.1. *Pachygnathus villosus* Dugès *in Oken*, 1836

*Pachygnathus villosus*. - Dugès *in Oken*, 1836, for a complete list of older references, see above under *Pachygnathus*.

*Pachygnathus ornithorhynchus* Grandjean syn. nov. - Grandjean, 1936: 398, comparisons between non-specific characters; Grandjean, 1937c: 202, Fig. 8A-E, Unchecked and Material and Remarks (16); Thor & Willmann, 1941: 139; Willmann, 1951: 136, Unchecked; Strenzke, 1953: 644; Delamare Deboutteville, 1960: 267, comparisons like in Strenzke (1953); Krivolutsky et al., 1978: 96, Fig. 302sh-i after Zachvatkin (1949); Kethley, 1990a: 675, 678, Remarks (15); Lindquist & Palacios-Vargas, 1991: 356.


(Figs. 52-59)

Grandjean did not designate a holotype, see Material. The description and figures by Grandjean (1937c) are diagnostic enough to identify *Pachygnathus ornithorhynchus* and consider the species as a junior synonymy of *P. villosus*, as suggested by Grandjean (1939: 3). Although European specimens are at hand, a neotype is not designated because there is no material available from type locality or even from southern France.
Differential diagnosis. This species can be segregated from other species by its slightly undulating soft integument (Fig. 54), setae vi being on prodorsal shield (Fig. 52) (not on separate microsclerites), and presence of two solenidia on femora I (Fig. 56), instead of five or seven.

Description. Length 320-505 µm (Fig. 53); soft integument slightly undulating (Fig. 54); prodorsal naso and sensillar area connected by broad sclerotic band filling up entire distance between setae vi, one pair of setae on in-area, setae exp anterior to eye lenses (Fig. 52); no cheliceral setae; rutella small with four tiny lobes distally, two pairs of adoral setae (Fig. 58); palps with four eupathids (Fig. 55); genital setae 14-18 per valve; anal setae 5 per valve; solenidial formula as given below, femora I with two solenidia (Fig. 56, Remarks 16).

Pachygnathus villosus has been collected near river banks and marine coastline from the Danube to the Mediterranean Sea.

Records. Austria, bogfields 140-180 m, 7 May and 13 Aug. 1939, 7 ex., in Willmann (1951) 2 ex. on slide Z8/0-5 as Pachygnathus ornithorhynchus, det. C. Willmann at ZSS.


Unchecked published records. France, Menton, Alpes Maritimes, 2 females and 2 males, in Grandjean (1937c), Remarks (16).

Remarks. 16. The number of solenidia may vary. A specimen of the Italian population on the east bank of the Gulf of Genova had three piliform solenidia on the left genu I and two on the right genu I. Grandjean (1937c) observed 4 specimens from Menton, France, and reported no solenidia on telofemora IV, but there might have been one piliform solenidion present next to a tuft of setal cilia (Fig. 59), as in all the species examined by me. This is the only difference between the members of the French population on west banks of the Gulf of Genova and the Italian (and Austrian) specimens, but considered to fall in the range of intraspecific variation.

4.5.2. Pachygnathus wasastjernae sp. nov.

(Figs. 3, 7, 60-67)
Holotype from Finland, Vaasa, on SEM-mount U145 at ZMT, see Remarks (17) and Chapter 9.1.

Differential diagnosis. This species can easily be segregated from other species by two pairs of setae on prodorsal in-area (Fig. 60), setae vi being on separate microsclerites (instead of prodorsal shield), and 5-7 solenidia on femora I (instead of two).

Description. Length 520 µm (Fig. 61); lamellar rows on soft integument strongly undulating (Fig. 62); prodorsal naso and sensillar area connected by sclerotic band, setae vi on separate microsclerites, extra pair of setae on in-area, setae exp anteromedially to eye lenses (Fig. 60); no cheliceral setae (Fig. 3); small rutella with tiny lobes (Fig. 66), two pairs of adoral setae; palps with five eupathids (Fig. 63); genital setae...
20-24 per valve (Fig. 7); anal setae 7-8 per valve (Fig. 7); solenidial formula as given below, 5-7 solenidia on femora I (Figs. 64, 67).

**Protonymph** (n=1)
- length 200 μm
- cleavage line
- slight neotrichy
- six pairs of prodorsal setae (instead of 7 pairs)
- integument strongly undulating
- one pair of genital setae
- only 2 solenidia on femora I

So far Pachygnathus wasastjernae has only been collected on surroundings of the Baltic Sea.


**Unchecked published records.** Poland, in Jesionowska, 1996, Remarks (18).

**Remarks 17.** The species name is a patronym in honour of the first Finnish acarologist F.D. Wasastjerna (1786-1853) who used to live and work in Vaasa (Hanski & Nuorteva, 1982; Uusitalo, 1995).

**Remarks 18.** I have not seen specimens of this species from Poland, but the setae vi are not inserted on the prodorsal shield in the Figure 6 of larval dorsum (Jesionowska, 1996: 329), which is the only specific character state of diagnostic value in the figure and text. The additional pair of setae on the in-area is missing both on larvae and on protonymphs of this species, but the identification could be verified by the form of integument.

Observed numbers of solenidia in Pachygnathus on legs I-II-III-IV:

<table>
<thead>
<tr>
<th></th>
<th>tarsi</th>
<th>tibiae</th>
<th>genua</th>
<th>femora</th>
</tr>
</thead>
<tbody>
<tr>
<td>villosus</td>
<td>2-1-0-0</td>
<td>3-2-2-0</td>
<td>2-3-2-2-1</td>
<td>2-0-0-0-1+0</td>
</tr>
<tr>
<td>wasastjernae</td>
<td>2-1-0-0</td>
<td>3-2-2-0</td>
<td>3-2-2-1</td>
<td>5-7-0-0-1+0</td>
</tr>
</tbody>
</table>

**4.6. Amphialycus Zachvatkin, 1949**


*Orthacarus* syn. nov. - Zachvatkin, 1949: 292, Remarks (19); Krivolutsky et al., 1978: 93, key of genera.

For a complete list of entries, see also under included species.

Type species by original designation *Amphialycus pentophthalmus* Zachvatkin, 1949 from the Ukraine.

The original diagnosis of the genus *Amphialycus* by Zachvatkin (1949) includes a solenidial formula of the type species, but the formulae of *Pachygnathus s.st.*-
species above and the formulae reported by Grandjean (1937a,c,d) show that solenidial numbers may vary interspecifically, which Grandjean (1936) also emphasized. Nor can the anterior position of the proximal solenidion o2 on tarsi I in relation to the lyrifissure be used in defining a genus - the position may vary intraspecifically (Figs. 88-89), and there is an undescribed species ‘olo’ of Pachygnathus from Polynesia which also has the solenidion anterior to the lyrifissure.

In addition, Zachvatkin’s generic diagnosis includes formulae of palpal and pedal setae, but P. villosus (= P. ornithorhynchus Grandjean, 1937) has a formula of palpal setae similar to that of A. pentophthalmus. Grandjean (1937a) reported setal numbers for the legs of Alycus roseus (= P. dugesi) only and the setal numbers of A. pentophthalmus do differ on some segments. Yet this character is no more reliable than the numbers of solenidia and palpal setae.

The (large) size proposed for definition of the genus may vary by up to ±300 μm intraspecifically, and females are larger, on these soft-bodied mites. Zachvatkin failed to report number and sex of the checked specimens, and a difference of 100 to 200 μm in size is still within the limits variation observed for other species of the family.

Distinctly two-coloured coloration of body (strongly pigmented proterosoma and legs, colourless hysterosoma) cannot be confirmed on specimens of an undescribed, closely related Polynesian Amphialycus ‘pac’ which have been in alcohol for some time. Coloration is not acceptable as a generic character because it easily fades and vanishes.

Also the form of posterior sensilla sci (= bp, coarser than the other prodorsal setae) is rather a species-specific character state (Grandjean 1937d), and finely, reduced number of adoral setae is shared with Alycus trichotus and Pachygnathus spp., and clear constriction after the seventh segment with the genus Orthacarus by Zachvatkin, 1949. The soft body also may swell up more or less during the preparation process (Fig. 72).

The only character state left from Zachvatkin’s original diagnosis (1949) is an unpaired frontal eye in place of the naso. This type of naso (an eye-like button) is also present in the undescribed species ‘pac’ from Polynesia mentioned above (Fig. 4). Zachvatkin (1949: 296) transferred Pachygnathus leucogaster Grandjean, 1937 to the genus Amphialycus and most of the characters of leucogaster do fit with those of Amphialycus pentophthalmus, except for the prominent naso of leucogaster (Fig. 71), which was perhaps missed by Zachvatkin because Grandjean did not depict the prodorsum of P. leucogaster.

Notwithstanding the remarks above, beside Alycus and Pachygnathus, there is a third evolutionary line which reflects a sort of tendency to adapt to a more edaphic way of life, reaching its highest degree in Orthacarus tremli Zachvatkin, 1949. At the moment, due to lack of resolution in the relevant part of the cladogram, I consider it premature to abandon the old name Orthacarus, which is tentatively considered as a subgenus here (see Remarks 19). The old genus-name Amphialycus is worth preserving for the species with elongated, but robust chelicera, although none of the characters of the original diagnosis is suitable for a new definition.

In addition to the three European species (A. pentophthalmus, A. leucogaster and A. oblongus) described below, an undescribed species at each of the collections of myself, ZMT, OSU and PU, from Asia, Polynesia, North America and South Africa, respectively, belongs here.

New synapomorphic character states have been presented to redefine the genus in Section 4.3. and more completely below.
Differential diagnosis. The genus can easily be segregated from the other genera of the family by the elongated and robust chelicera (Figs. 4, 5), finely striated anterior pair of lateral eyes (Fig. 75) (glabrous in one case), and palpal microtrichious eupathids which may be separate or basally fused (Figs. 77, 85).

Description. Length 300-600 µm; soft integument with slightly winding, contiguous and parallel ridges, transverse lamellae almost even in size and in regular intervals on ridges (Figs. 72, 73, 84); surface of anterior eye lenses with fine ridges (Fig. 75) (one exception), a pair of setae in pubescent and relatively long like caudal setae (Figs. 68, 71, 72, 86); cheliceral shafts elongated but robust, evenly tapering towards digits, teeth of digits few and strong (Figs. 4, 5, 74); rutella adaxially concave, blunt, distally forming a lobed, spoon-like membrane (Figs. 4, 70, 74, 79); four (sometimes five) microtrichious eupathidia on palpal tarsi (Figs. 69, 77, 78, 85); combined coxal fields III and IV not enlarged medially, trochanters normal, empodia densely setulated (Fig. 81); additional eupathids on tarsi I.

Remarks 19. Zachvatkin (1949) created a new genus for Orthacarus tremli [= Amphialycus (Orthacarus) oblongus of this work] on basis of prodorsum and body form. Yet Orthacarus does not come out in the analysis as monophyletic and the question is rather of an ultimate end in a transformation series towards better adaptation for living in soil system as manifested in edaphomorphisms, such as (1) smaller size, (2) elongated body, (3) shorter setae, and (4) terminal anus. There is also this tendency to decreasing distance between palpal eupathids among the various members (some undescribed) of Amphialycus s.s. The eupathids become closer to each other and finally fuse, as in the case of tremli. The second character state to separate the subgenus Orthacarus is nasolessness and the consequent approach of the counterparts of setae vi. The members of the Amphialycus s.s. have a naso, and counterparts of the setae vi are as far from each other as are the counterparts of the sensilla ve. Because the cladogram is not fully resolved, I have preferred at this early point of revision to conserve the old name Orthacarus, but reduce it in rank to a subgenus of Amphialycus.

4.6.1. Amphialycus (Amphialycus) pentophthalmus Zachvatkin, 1949

Amphialycus pentophthalmus. - Zachvatkin, 1949: 295, Figs. 6-9, Harkova, the Ukraine,
Unchecked: Krivolutsky et al., 1978: 94, Fig. 301e-s after Zachvatkin (1949).
(Figs. 68-70 copied from Zachvatkin 1949: 293)
A holotype was not designated, see Material.

Differential diagnosis. This species is closely related to an undescribed Polynesian Amphialycus-species 'pac’ but can be segregated at least by solenidial pattern. The prodorsal naso is a small, roundish eye-like button, unlike that of other European species. The diagnosis of this species is based on Zachvatkin's text and figures because new material was not available.

Description. Prodorsal naso small, roundish eye-like button (Fig. 68); one pair of smooth cheliceral setae abaxially; rutella widen to round hyaline membrane with two lobes apically, one pair of adoral setae, smooth and tapering (Fig. 70); four palpal eupathids clearly apart from each other (Fig. 69); solenidial pattern as given below, tarsi I and II have 2 solenidia (instead of 3); ω2 closer to ω1 than to lyrifissure on tarsi I; tibiae III with 2 solenidia (instead of 1) and genua III with 1 solenidion each (instead of 2).
The type locality of only once collected *Amphialycus pentophthalmus* on steppe soil is hardly above see level in the Ukraine (cf. *A. leucogaster*). The species also has a close relative in Polynesia.

**Unchecked published records.** The Ukraine, Harkova, surface layer of soil, in Zachvatkin (1949), see Material.

4.6.2. *Amphialycus (Amphialycus) leucogaster* (Grandjean, 1937)

*Pachygynathus leucogaster.* - Grandjean, 1936: 398, comparisons between non-specific characters; Grandjean, 1937d: 262, Fig. 9A-D, Menton, Alpes-Maritimes, France, Unchecked and Material; Thor & Willmann, 1941: 140; Krivolutsky et al., 1978: 96, Fig. 302k after Grandjean (1937d).


*Pachygynathus arhinosus* Willmann syn. nov. - Willmann, 1953: 478-479, Fig. 22a-e, several females, Records and Remarks (21).  
*Pachygynathus villosus* Dugès, 1836. - Schweizer & Bader, 1963: 251, Fig. 46a acc. Dugès (1834b) and Figs. 46b-h acc. Berlese, Remarks (20).

(Figs. 71-81)

A holotype was not designated, see Material.

**Differential diagnosis.** This species can easily be segregated from the other species of *Amphialycus* by prodorsal pattern (Fig. 71) and solenidial formula.

**Description.** Length 350-610 μm (Fig. 72); around 30 relatively short barbs on mid-dorsal setae, caudal setae elongated, ventral and pedal setae and their barbs elongated (Figs. 72, 73, 80); prodorsal naso flat, long and broad with a clear margin-strip, setae *vi* sparsely barbed, clearly longer than setae *sce* and *exp*, setae *in* densely barbed like caudal setae (Figs. 71, 72, 76); one pair of smooth chelicerat setae abaxially (Fig. 74); rutella widen to a round hyaline membrane with two lobes apically, two pairs of adoral setae: abaxial ones being rudimentary (Figs. 74, 79); four to five palpal eupathids clearly apart from each other, distal part of palpal integument with short transverse lamellae instead of having contiguous annular rings (Figs. 77, 78, left and right palp of the same specimen!); genital valves each bearing 21-34 genital setae externally; anal setae 5-11 per valve; solenidial formula as given below, o2 usually anterior to lyrifissure on tarsi I (Fig. 80), famulus II with some proximal barbs (Fig. 81).

*Amphialycus leucogaster* has its so far verified distribution in rocky places of montane areas in the Alps and the Apennines (cf. *A. pentophthalmus*).

**Records.** Austria, Weissenbachgraben bei Gstatterboden im Gesäuse, 17 Nov. 1951 CW: 2 females, 1 tritonymph (lectotype here designated) as *Pachygynathus arhinosus* at ZSS, Remarks (21); Styria, Bruck a.d. Mur, ESE Mixnitz, "Buchebeben", meadow with rocks, here and there *Fagus silvatica, Picea abies* and *Pinus silvestris*, SW, 1055 m, rock, mosses, 1 April 1993 GK: 16 ex. (sample KR-295) of which 3 ex. on U350, the rest in tube and 29 May 1996 GK: 17 ex. (sample KR-380) of which 3 ex. on U341, the rest in tube; Salzburg, Lungau, Muhr, "Steppenhang", rocky wall at the top of a dry slope, mosses, lichens and *Sempervivum* sp., S, 1300 m, rock, mosses, 26 August 1993 GK: 1 ex. (sample KR-316), U347.
Italy, Col d'Oreia, Montalcino, Siena, on spontaneous herbs of the vineyard floor, 20 April 1994 RN: 2 ex. as *Pachygnathus* sp.2 at ISZA.

Switzerland, Alpen, Furcla Trupchum, 2786 m, under stone, 11 August 1929 JS: 1 ex. as *Pachygnathus villosus/Alycus roseus* on slide N226 at NMB, **Remarks (20).**

Unchecked published records. France, Menton, Alpes-Maritimes, in Grandjean (1937d) several ex., see **Material.**

**Remarks. 20.** The specimen as *Pachygnathus villosus/Alycus roseus* on slide N226 at the Schweizer Collection, NMB is in several pieces under two adjacent cover classes. Most parts are inside air fingers and difficult to observe but determination can be based on chelicera, one palpal tarsus, genital area, and setae and solenidial position on leg I. The record by Schweizer (1951) as *Pachygnathus roseus* is the same as the record of *Pachygnathus villosus* in Schweizer & Bader (1963), but the Figure 46b-h on page 251 as *Pachygnathus villosus* ex Berlese (1887) refers to *Alycus trichotus*, see **Remarks (7).**

**Remarks 21.** Two females and one tritonymph in the syntype series of *Pachygnathus arhinosus* at ZSS was examined by me using a phase-contrast microscope. Willmann did not designate a holotype. The females with eggs are intact on two slides, but the tritonymph is in several pieces and under a square cover glass with legs, gnathosoma and hysterosoma apart and it is quite likely that the description is based on this tritonymph. This would explain the 8 segments which Willmann uses as the main characteristic to separate *P. arhinosus* from *P. leucogaster*: see Kethley (1990a) concerning anamorphosis. Only the ventral area and one leg can be observed with sufficient accuracy, the other parts are badly damaged, fragmented or inside air-fingers. The subjective synonymy above is based on: (1) 33-34 genitals, (2) tens of empodial rays, (3) several eupathidia on tarsi, (4) elongated chelicera, (5) ? one cheliceral seta, (6) ? long, broad naso, (7) length 450 μm.

### 4.6.3. *Amphialycus (Orthacarus) oblongus* (Halbert, 1920) comb. nov.

*Alicus oblongus.* - Halbert, 1920: 140, pl. 23, Figs. 23a-c; Grandjean, 1936: 398, erroneous orthography of *Alycus* C.L. Koch, **Records and Remarks (22).**


*Orthacarus tremli* Zachvatkin *syn. nov.* - Zachvatkin, 1949: 292, Figs. 1-5, **Unchecked and Remarks (23);** Krivolutsky et al., 1978: 94, Fig. 301a-d after Zachvatkin (1949).

*Orthocarus tremli.* - Jesionowska, 1996: 330, Fig. 7, misspelling, **Remarks (24).**

*Alycus ? roseus.* - Womersley, 1944: 139, **Material, Unchecked and Remarks (25).**

(Figs. 5, 82-89)

Holotype from Malahide, Ireland from orange lichen zone at NMI was examined by me using a light microscope.

**Differential diagnosis.** This species can be segregated from other species of *Amphialycus* by having four basally fused palpal eupathids, missing naso, strongly reduced pair of setae *vi*, exceptionally closely inserted to each other (Fig. 82).

**Description.** Length 300-500 μm (Fig. 83); dorsal setae sparsely ciliated (Fig. 84); setae *vi, sce and exp* reduced in size, naso missing, distances between counterparts of setae *vi* and anterior bothridial sensilla *ve* less than distance between setae *in* (Fig. 82); one pair of smooth cheliceral setae abaxially (Fig. 5); rutella widening to a round hyaline membrane with two lobes apically (Fig. 5), one pair of adoral setae; palpal tarsi elongated, narrow with four fused eupathids apically (Fig. 85); 14-18 genital setae per valve; anal valves terminally with 7-8 setae (Figs. 83, 86); solenidial formula as given below, famulus on tarsi II with three barbs (Figs. 5, 87, 88).
**Larva** (n=2)
- 180-240 μm
- 3 anal setae per valve
- 1-1-0 2-2-2 3-2-0 1-0-0

**Protonymph** (n=2)
- 270-280 μm
- genital setae 1 per valve
- 2-1-0-0 2-2-2-0 3-2-0-1 1-0-0-0

**Deutonymph** (n=2, Fig. 86)
- 200-300 μm
- genital setae 3-5 per valve
- 2-1-0-0 2-2-2-0 3-2-0-1 1-0-0-0

`Amphialycus (O.) oblongus` has been reported not only around Europe (excluding Fennoscandia), but might have an anthropochorous distribution on other continents as well (see Remarks 25). In spite of several edaphomorphisms in its appearance, this species has so far been collected most often in moss.

**Records.** Ireland, Station, orange lichen zone, 24 May 1915 JH: 1 ex., in Halbert (1920): *holotype* as *Alicus oblongus* on a slide, at the Halbert Historical Collection, NMI, Remarks (22).

Italy, Florence, Boboli Garden, moss, 9 July 1992 MU: 17 ex., U14, U15, U16, U321, and in tube, ZMT; Montalcino-Siena, on spontaneous herbs of the vineyard floor, 20 April 1994 RN: 2 ex. (1 eggless female, one with 3 eggs) as *Pachygnathus* sp.1, ISZA; 25 July 1994 RN: 12 ex. (5 larvae, 4 PN, 2 DN, 1 female with 3 eggs) as *Pachygnathus* sp.1 at ISZA; 6 June 1996 RN: 8 ex. (1 DN, 1 ex. eggless female, 3 ex. with 1 egg, 2 ex. with 3 eggs, 1 ex. with 4 eggs) as *Pachygnathus* sp.1, ISZA.

Unchecked published records. Poland, in Jesionowska (1996), Remarks (24);

The Ukraine, Harkova, surface layer of soil, 3 females, in Zachvatkin (1949), Remarks (23).

Australia, twelve miles north of Quorn, Mount Arden, moss, in Womersley (1944) 2 ex. as *Alycus ? roseus*, Material and Remarks (25).

Remarks 22. Well sealed under a round cover glass, the holotype of *Alicus oblongus* at NMI is mounted on its back, has lost some leg segments and the prodorsum is not properly observable. However, the following can be noted: 3 pairs of genital discs, caudal anus, small setae, elongated chelicera, palpal eupathids basally fused and two solenidia on tibia II. In addition, Figs. 23a and 23b of Halbert (1920) show the following combination of characters: lateral eyes present, naso missing, sensilla ve exceptionally close to each other, palpal eupathids basally fused, and one cheliceral seta abaxially. There is a good reason to expect that the species (originally described from two specimens from orange lichen zone) belongs to a morphospecies which probably has a wide distribution, see Remarks (25). As the oldest synonym, the name *oblongus* must be adopted for the species according to the Code.

Remarks 23. The description of *Orthacarus tremli* by Zachvatkin (1949) differs in two respects from the Italian material of *A. oblongus*. Zachvatkin’s (1949: 293,
Fig. 2) drawing of the anterior limit of the prodorsal sclerite shows the setae \( vi (=bf) \) and \( ve (=ba) \) apparently inserted on soft integument, but this is hardly the case because the anterior hood is subject to invagination. The setae of Italian specimens are on prodorsal shield. Secondly the solenidial number on leg III (p. 295) is reported to be 0-1-1-1 for tarsus-tibia-genu-femur, respectively. The formula is assumed to be erroneous because even if the alycins are primitive, it would be unique among the extant species both to have a solenidion on femora III and secondly, to have a claviform/baculiform solenidion on tibia III without a ceratiform/piliform partner. The solenidial formula of leg III on Italian specimens is 0-2-0-0.

**Remarks 24.** A specimen identified as *Orthocarus tremli* by Jesionowska (1996: 330, Fig. 7) is conspecific with the Italian material of *A. oblongus*.

**Remarks 25.** Van der Hammen (1969: 193) supposed the Australian *Alycus ? roseus* to represent a nymph of a species different from *Alycus roseus*. The description and the specimen illustrated by Womersley (1944: 139, Figs. 3F-I) present characters like those of *A. oblongus* (prodorsum, palpus), but a comparison with fresh material is required. The conspecificity is quite possible because it appears that the species may have a wide distribution. I have seen some slides and sketches of South African specimens drawn by Prof. P. Theron, with the subgeneric character states at least, and also the solenidial formula seems to be identical with the formula of Italian specimens, but more exact information will be published in another context.

Observed number of solenidia in the described species of *Amphialycus* on legs I-II-III-IV:

<table>
<thead>
<tr>
<th></th>
<th>tarsi</th>
<th>tibiae</th>
<th>genua</th>
<th>femora</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>pentophthalmus</em></td>
<td>2-2-0-0</td>
<td>2-2-2-0</td>
<td>3-2-1-1</td>
<td>2-0-0-0</td>
</tr>
<tr>
<td><em>leucogaster</em></td>
<td>2-1\2-0-0</td>
<td>2-2-2-0</td>
<td>3-2-2-1</td>
<td>2-0-0-0\1</td>
</tr>
<tr>
<td><em>oblongus</em></td>
<td>2-1-0-0</td>
<td>2-2-2-0</td>
<td>3-2-0-1</td>
<td>1-0-0-0</td>
</tr>
</tbody>
</table>

### 5. Taxonomy of European Bimichaeliini

#### 5.1. Introduction

Eleven nominal species (out of 25 on a global basis) have been included in the genus *Bimichaelia (sensu lato)* from Europe alone, though Thor & Willmann (1941) wrote that the species of *Bimichaelia* are so alike that it is very difficult to segregate them from each other. In fact the European species (and the genera) are very distinct, but because of insufficient descriptions from other continents, relationships between and within the proposed genera remain speculative. Nevertheless, some trends can be outlined, e.g. by primary and secondary patterns of integument (Fig. 1 and Section 5.3.).

As to the European fauna, *Michaelia augustana* Berlese, 1884, *M. setigera* Berlese, 1905, and *M. subnuda* Berlese, 1910 have been described from Italy. *B. setigera* var. *sarekensis* Trägårdh, 1910 from Sweden was raised to species status by Grandjean (1943). In a series of papers (1942-43) he also described *B. arbusculosa*, *B. campylognatha* and *B. diadema* from France. Earlier, Halbert (1923) had described *B. crassipalpis* from Ireland, and later Willmann (1953) proposed *B. rectangula* from Austria.
and *B. praeincisa* Willmann, 1956 from Poland while Mihelčič (1956) still added *B. ramosa* from Spain. The number of Bimichaeliini-species in Europe is here reduced to five.

Subfamily Bimichaeliinae Womersley, 1944

Alychidae Berlese, 1885: 134, in part (only *Michaelia*, preoccupied name); G. Canestrini, 1891: 18, in part (only *Michaelia*, preoccupied name), erroneous orthography.

Eupodidae? Thor, 1902: 165, in part (only *Bimichaelia*, new name for *Michaelia*), unjustified replacement.

Alycidae Thor, 1925: 263; Judson, 2000: 533, in part (only *Bimichaelia s.l.*, only).

Pachygnathidae (not Menge, 1866) Grandjean, 1939: 3, in part (only *Bimichaelia s.l.* only).

Bimichaelinae Womersley, 1944: 133, new subfamily for *Bimichaelia s.l.* only.

Bimichaelidae Kethley, 1982: 118, in part (only *Bimichaelia s.l.* only), erroneous orthography.

Bimichaeliidae OConnor, 1984: 22, in part (only *Bimichaelia s.l.* only); Kethley, 1990a: 670, key, in part (only *Bimichaelia s.l.* only).

See also synonymy under Alycidae in Chapter 1.1.1. and below under Bimichaeliini (=*Bimichaelia sensu lato*).

Type genus: *Bimichaelia* Thor, 1902

Traditionally, the subfamily Bimichaeliinae Womersley has been identical to the genus *Bimichaelia sensu lato*. This state of affairs has prevented a discussion of evolutionary lines existing within the group. The material from South Africa, which will be described in collaboration with Prof. Theron, includes a species ‘*sil*’ (see Appendix 3), so exceptional in character states, that it alone forms a sister group of the Bimichaeliini. The tribe Bimichaeliini, which includes the rest of the world fauna, is now identical to *Bimichaelia s.l.* and discussed in this work.

5.2. Bimichaeliini Womersley, 1944 new rank

Tribe Bimichaeliini Womersley, 1944 (=*Bimichaelia s.l.* Thor, 1902)


Bichimaelia. - Grandjean, 1943: 1, misspelling.


Unchecked published records. Czech Republic, Haberwiesen, Borstengrasmatte (1200 m), nach S geneigt, in Frenzel (1936), Material. Poland, Warsaw, in Niedbała et al. (1982). Republic of South Africa, soil under Acacia karroo, in Meyer & Ryke (1966); RSA, Theron (1979) several spp. in several genera will be published in another context. I have seen a small sample of slides, for comparisons. Canada, Quebec, woodland humus, 9 ex. and 170 ex. of 2 spp., in Marshall & Kevan (1964).

USA, south, in Baker & Wharton (1964); USA, S.Ca., Broomsedge and Lespedeza fields, in Wiegert (1974); PA, untreated Old field-White Spruce Community and Mixed-Oak Hardwood soils, in Dindal & Norton (1979); HI, in Goff (1983); PA, grape vineyard, in Jubb et al. (1985); Colorado, Larimer County, Douglas-fir and ponderosa pine needle litter, in Walter (1988) 2 spp..

China, Jingyuetan region, Changchun city, in Peng et al. (1988).

Type species by original designation: Michaelia augustana Berlese, 1884 from Mt. St. Augusta, Treviso, Italy. The holotype at BA was examined by me using a phase-contrast microscope.

The detailed description of Bimichaelia s.l. by Grandjean (1943: 18-35) was based on three French species, but he ignored the fourth one, B. subnuda with an exceptional external morphology, even if it was briefly mentioned on page 22. In the revised description of the tribe Bimichaeliini below, the world members described so far, and several undescribed species examined by me have been taken into account. The synapomorphies outlined in Chapter 3.1 for Bimicialiinae also fit well for Bimichaeliini, except that the large lamellae are either in clumps or in rosettes and not simultaneously present as in the African sister group (Appendix 3).

Differential diagnosis. This lineage and tribe can easily be segregated from the tribes of Alycini, Petralycini and other Endeostigmata by their intricate dorsal pattern of large lamellae (Figs. 95, 105, 115, 125), posterior pair of prodorsal sensilla (sci) being globular (Fig. 100) and stylet-like chelicera (Fig. 123).

In addition to the synapomorphies, outlined in Chapter 3.1 (for both subfamily and tribe) the species of this tribe have: 1. only insertion points of setae sclerotized (i.e. microshields around setal basis are not so obvious); 2. posterior pair of lateral eyes lost; 3. cheliceral setae lost (present in the sister group); 4. rutella lost; 5. more than one solenidion on tarsi I and II; 6. clawless empodia in all stages (Fig. 99).

Description. Small (European species ca. 500 μm) to large (up to 2000 μm); white; hysterosoma soft, segmented, neotrichous in adults; strongly ornamented idiosomal cuticle: primary pattern by large lamellae forming either cells (loops/polygons) or separate clumps (Figs. 100, 110); secondary pattern either by small lamellae forming parallel lines or by (prelamellar) granules (Figs. 105, 125); shaft of dorsal setae acicular, barbed with basal cilia, lancet-like or plumose (Figs. 95, 115, 125, 135); naso button-like, transversely grooved (Fig. 96, a frontal eye proposed to be on ventral side of naso (Grandjean, 1943) not confirmed so far by SEM); lateral eyes missing; posterior sensilla sci globular (Fig. 104); anterior pair of sensilla ve filamentous (Fig. 94); chelate chelicera elongated into stylet-like elements (Fig. 123), outer edges of digits smooth (Fig. 102), inner edges of movable digits with tiny rake-like serration, yet ‘teeth’ being (Fig. 122): transversely
orientated, sharply pointed, separated, with regular distances, in one row (obviously in
most cases, but usually digits are closed and serration is not observable by SEM-
technique), inner sides of both shafts concave, forming a tube when intimately adnated
(Fig. 124), cheliceral setae missing (Fig. 123); rutella missing; subcapitulum elongated
(Fig. 92); adoral setae missing; palpi with an apical solenidion in contact with one or two
eupathids (Figs. 97, 119); supracoxal setae ep missing; supracoxal setae el missing; femora
IV undivided; eupathids (pseudacanthoids) ventrally on both tarsi I and II (Fig. 134);
setulate empodia clawless (Fig. 99); famulus I present (Figs. 99, 113, 127, 133); famulus II
missing; for distribution of various types of solenidia, see formulae at the end of Chapter 5.

5.3. Key to the European genera and species of Bimichaeliini

The key of the five species known from Europe is based on previous descriptions, the slide
material available and the fresh material collected for the purpose. The quest for character
states which distinguish the European fauna from close relatives on the other continents
revealed that some characters used up to now in the identification work of species, like
pattern of large lamellae (primary pattern) and baculiform solenidia, but also new
characters like secondary pattern (the pattern in between large lamellae), instead delineate
larger entities which are suitable for establishing either new generic taxa or recognizable
species groups which may be helpful in recovering and regrouping specimens from other
continents and old collections. The analysis of character states for the world fauna at this
moment does not allow clear answers concerning relationships of the species and groups
inside the two genera presently recognized in the European fauna. Instead, the species can
be characterized by using form, number and position of ceratiform/piliform solenidia and
form of setae and sensilla. A phylogenetic tree is given in Fig. 1.

Lineage VII. Bimichaelia s.st. This minor group can be defined by one progressive and
one regressive states.

2/1. Presence of secondary pattern of granulae on skin (Figs. 95, 105). An independent
appearance of dense granulation (and small lamellae) is supposed in the subnuda-group.
13/2. Reduction of dorsal setae (Figs. 95, 105). Dorsal setae have a low number of cilia
per seta, some of them reduced to a few basally inserted barbs only.

Lineage VIII. Laminamichaelia. This sister-group of Bimichaelia can be defined by five
progressive synapomorphies. Presence of small lamellae on secondary pattern is common
to all members, but at the moment the lineage is large, diverse and includes several
undescribed or poorly known species which later may deserve they own lineage.

0/2. Enlargement of adult stage. Most tropical members of this genus are enlarged in
both length and width but reversal in size of the smaller species has also happened. The
three European species are either small or medium-sized (Figs. 111, 121, 131).

3/1. Presence of small lamellae transversely on ridges (Figs. 115, 125, 135). Secondary
pattern consists of either parallel rows of tightly packed, small lamellae inside cells or the
lamellae are sparsely spread, not so well developed and along with granulae. An
undescribed species ‘mau’ from Polynesia have the lamellae lined up longitudinally one
after another.

14/2. Presence of tripartite crista (Figs. 120, 132). The area from naso to anterior pair of
sensilla is strongly sclerotized with a middle track and two narrow stripes like sidewalks
on each side but the degree of sclerotization may vary and even be missing (Fig. 110),
which character state rather can be considered quite primitive, see Chapter 3.1.
34/4. Presence of additional setae on prodorsum’s soft and hard integument (Fig. 130). If neotrichy is insignificant and only a few additional setae are present, they are always inserted laterally on soft parts (e.g. setigera-group, Fig. 120). Most tropical species have extra setae also on sclerotized area between the sensilla, and crista is hairy only on most neotrichous species. Sclerotization is insignificant and additional setae are missing in the subnuda-group (Fig. 110).
46/3. Support of palpal solenidion by both eupathids (Grandjean, 1943: 39, Figs. 12B, 12C). The two TP-type eupathids are attached ventro-laterally to apical solenidion. This character state of arbusculosa-group can also be found in the subnuda-group (Fig. 119) but is missing in the setigera-group (Fig. 123).

Key to the European fauna

The solenidial numbers concern the adult stages.

1. - Primary pattern of large lamellae by clumps in parallel rows on dorsal integument (Figs. 110, 111); secondary pattern a mixture of granules and small transverse lamellae (Fig. 115)... subnuda-group of Laminamichaelia.
   3a. - Two baculiform solenidia side by side on tibia I (Fig. 114); two baculiform solenidia on tibia II less than half of segment in length (Fig. 116)... subnuda.
- Primary pattern cellular (Figs. 91, 101, 121, 131)....2.
2. - Secondary pattern granular (Figs. 95, 105); prodorsum holotrichous (six pairs of setae only) (Figs. 90, 100).... Bimichaelia s.st.
   2a. - dorsal setae with a few basal barbs subequal in length and clearly shorter than the acicular main cilium (Fig. 90); adult ca. 500μm in length (Fig. 91)... augustana.
   2b. - two to three of a few basal barbs clearly longer than the other barbs (Fig. 100); adult ca. 300μm in length (Fig. 101)... sarekensis.
- Small lamellae of secondary pattern transversely (Figs. 115, 125, 135); prodorsum neotrichous (Figs. 120, 130).... Laminamichaelia new genus....3.
3. - Additional setae only on lateral rims of prodorsum or soft integument (only one pair of setae on sclerotized in-area) (Fig. 120); two baculiform solenidia on tarsus I, two baculiform solenidia obliquely on tibiae I, II and III (Figs. 123, 126).... setigera-group.
   3b. - most of the dorsal setae lancet-like (Fig. 121); an S-shaped solenidion on tarsus I (Figs. 123, 127); two to three piliform solenidia on femur I (Fig. 123)... setigera.
- Additional setae inserted all over prodorsum, i.e. on both soft integument and sclerotized parts (area of setae in) (Fig. 130); three baculiform solenidia on tarsus I (Fig. 133), two baculiform solenidia side by side on tibiae I, II and III (Figs. 136, 137, 138).... arbusculosa-group.
   3c. - anterior pair of sensilla ve branched (Fig. 130); adult less than 500μm in length (Fig. 131)... arbusculosa.

5.4. Bimichaelia s.st. Thor, 1902

Michaelia Berlese, 29 Dec. 1884; A. M. S. fasc. 16 no. 6, text and pl., note: "Nov. gen. et spec." on the wrapper, nom. praecocc. (not Trouessart, Nov. 1884; not G. Haller, 18 Dec. 1884); Ewing, 1913: 125.
Bimichaelia Thor, 1902: 165 as a nomen novum for Michaelia Berlese, 1884 (preoccupied);
Trägårth, 1910: 468; Grandjean, 1943: 18, in part (augustana and sarekensis = campylognatha only).
For a complete list of entries, see also under each species.
Type species by original designation: *Michaelia augustana* Berlese, 1884 from Mt. St. Augusta, Treviso, Italy.

Besides *Bimichaelia augustana* (Berlese, 1884) from Italy, this genus also contains *Bimichaelia sarekensis* (Trägårdh, 1910) from Sweden with three new synonymies (see the list below) recorded from Ireland, France, Algeria, Austria and Poland, *Bimichaelia pallida* Ewing, 1913 from Oregon, USA, and an undescribed species ‘*bim*’ from Utah, USA (at the OSU Collection).

**Differential diagnosis.** The genus can be differentiated from other genera with holotrichous prodorsum (prodorsal setae *sce* and *exp* on the rim) by: dorsal setae, all dorsal setae have less than ten, mainly short barbs basally; primary pattern: by roundish to subpolygonal loops; and secondary pattern: both tiny ridges inside loops and skin between ridges are granular (Figs. 90, 95, 100, 105). These character states were previously listed in Section 5.3 for Lineage VII.

**Description.** Small to medium-sized (Figs. 91, 101); dorsal setae: less than ten, mainly short, barbs basally, ventral and pedal setae: several long barbs, dorsal primary pattern or the pattern of large lamellae: flanking constellations of 5-6 roundish loops around a seta, secondary pattern or the form and pattern of components along tiny ridges and space between the ridges inside loops of soft integument: granular (Figs. 92, 95, 103, 105); prodorsal naso narrowest at the base, enlarging distally, six pairs of prodorsal setae: anterior pair of sensilla (ve) simple, *vi*, *sce* and *exp* on the anterior rim, only one pair of setae on in-area, area between anterior sensilla and naso does not differ much from adjacent prodorsal integument, i.e. no clear crista-like pattern (Figs. 90, 96, 100, 106); chelicerae curved (Fig. 102); palps short and stout (Figs. 92, 102); palpal solenidion without a basal tubercle (Figs. 97, 102); of palpal eupathids (TP-sensilla, see Evans, 1992: 69), k" free and k' supporting solenidion (Figs. 97, 102); three baculiform solenidia on tarsi I (Figs. 98, 108); one baculiform solenidion on tibiae (instead of 2) (Figs. 93, 103); no baculiform on genu II; thin solenidia ceratiform (Figs. 93, 103); famulus I in distal position (Fig. 99); larvae holotrichous (Fig. 151).

### 5.4.1. *Bimichaelia augustana* (Berlese, 1884)

*Michaelia augustana* Berlese, 1884: A. M. S. fasc. (vol.) 16 no. 6 text, and pl. 41 Figs. 1-11, note: "Nov. gen. et spec." on the wrapper, Mount St. Augusta in Seravalle in Tarvisino, rare (1 ex.) in moss, **Records.** - Berlese, 1889 (1890 in Thor & Willmann, 1941): A. M. S. fasc. 57 no. 8, text and pl., **Records** and **Unchecked**; Berlese, 1893: 34-35, 134, pl. 4 Figs. 1, 4, 6, 8, 10; Berlese & Leonardi, 1901: 15; Berlese, 1904: 13; Baker & Wharton, 1964: 200.


*Alycus devius.* - Oudemans, 1937: 867, unjustified synonymization with a species inquirendae (see Chapter 8).

(Figs. 90-99)

Holotype from Italy, Treviso, Mount St. Augusta, at BA, examined by me using a phase-contrast microscope.

**Differential diagnosis.** This species can easily be segregated from other members of the genus by dorsal setae, a few basal barbs being subequal in length and
clearly shorter than the acicular main cilium (Fig. 95), weakly reticulate pattern of lamellar loops on prodorsal shield (Fig. 90), and the solenidial number on genu I being 3C (not 1C or 4C) (Fig. 93) and on genu II 3C (not 1C or 2C).

Description. Length 450-700 μm (Fig. 91); reticular primary pattern by flanking rosette groups of 5-6 roundish loops around the setae dorsally, dorsal setae acicular with a few short barbs basally (Figs. 91, 95); elsewhere also longer cilia on setae (palpi, legs and ventral side); pattern of large lamellae weakly reticulate from sensillar area to finely striated naso (some specimens from North America have clear reticulation), anterior pair of sensilla ve simple, sparsely barbed basally (Figs. 90, 94, 96); four pairs of subcapitular setae (Fig. 92); baculiform palpal solenidion supported by one eupathid, the other one being free, joint between palpal genua and femora complete (Figs. 92, 97); 15-17 genital setae per valve (Fig. 91, partly visible); 4-7 anal setae per valve; solenidial formula as given below, genu I with 3C solenidia (Fig. 93), genu II with 3C solenidia; famulus I abaxial to claws (Fig. 99).

The only confirmed records of *Bimichaelia augustana* are in wooded areas south of the Alps in Europe.


Italy, Treviso, Monte di Santa Augusta a Seravalle, moss, autumn 1884 AB: vial 6°/296: 1 ex. (holotype) at BA; Treviso, Orto Saccardo, forest, Oct. 1889 AB: slide 39/49: 2 ex. at BA; Treviso, Orto Saccardo, forest soil (sotto), no date AB: 40/1: 1 ex. at BA; Veneto, Treviso, Bosco del Cansiglio, litter of beech, 25 April 1986 PL: 1 ex., U319; Veneto, Treviso, La Crossette del Consiglio (1120 m), stumps of deciduous trees, 25 April 1986 PL: 1 ex., U320.


Italy, Treviso, Orto Saccardo, forest, Oct. 1889 AB: vial 6°/298: 5 ex. at BA; Venice, rotten wood, no date AB: slide 39/50: 2 ex. at BA, - obviously reported in Berlese (1889), 1890 in Thor & Willmann (1941): A. M. S. fasc. 57 no. 8, text and pl.: several ex. from forest, humid rotten and fresh wood in Tarvisino; Bergamo, no habitat, no date AB: slide 143/44: 1 ex. at BA.

5.4.2. *Bimichaelia sarekensis* Trägårdh, 1910


*Bimichaelia crassipalpis* Halbert syn. nov. - Halbert, 1923: 383, pl. 21, Figs. 22a, 22b; Grandjean, 1943: 19; Evans, 1953: 806; Remarks (27).

*Bimichaelia campylognatha* Grandjean syn. nov. - Grandjean, 1942: 110, general comparisons; Grandjean, 1943: 19, 44, Figs. 14A-E, 15A-D. Remarks (28); Alberti et al., 1981: 186, Fig. 15b, cuticular ultrastructure; Kethley, 1991: 131; Alberti & Coons, 1999: 646.


*Bimichaelia rectangula* Willmann syn. nov. - Franz, 1950: 82, nom. nud.; Willmann, 1953: 479, Fig. 23, Records and Remarks (29); Willmann, 1956: 233.

Bimachaelia setigera. - Schweizer & Bader, 1963: 253, same record as in Schweizer (1951), Fig. 48a acc. Berlese, Figs. 48b-d originals, Records, misspelling.

Bimachaelia crassipalpus. - Purvis, 1982: 393, misspelling.

(Figs. 100-109, Fig. 151 after Grandjean, 1943)

Holotype from Sweden, Sarek National Park, at NRM, is lost, see Material.

**Differential diagnosis.** This species can be separated from other members of the genus by dorsal setae having two or three of the basal barbs clearly longer than the others except for the longest main acicular cilium (Fig. 105), reticulate prodorsal shield between naso and anterior pair of sensilla (Fig. 100), imperfect joint between palpal genua and femora (Fig. 102). The solenidial number on genu I is 4C (not 1C or 3C) (Fig. 103) and 3C (not 1C or 2C) on genu II.

**Description.** Length 225-350 μm (Fig. 101); reticular primary pattern by flanking rosette groups of 5-7 roundish loops around a dorsal seta, dorsal seta acicular with two or three long and a few short barbs basally (Figs. 100, 101, 105); setae on palpi, legs and ventral side with several longer cilia (Figs. 102, 103); clearly developed reticulate pattern from sensillar area to striated naso, anterior sensilla (ve) simple, sparsely barbed basally (Figs. 100, 106); one pair of subcapitular setae; joint between palpal genua and femora incomplete (Fig. 102); 6-8 genital setae per valve (Fig. 107); 4-6 anal setae per valve; solenidial formula as given below, genu I with 4C solenidia, genu II with 3C solenidia, see Remarks (26), famulus I abaxial to claws, in the same position as in Fig. 99, overlooked by Grandjean (1943: 31).

**Bimichaelia sarekensis** seems to live in the Alps and to the north and west of them, in coniferous forests and montane birch stands.

**Records.** Austria, Admont, no habitat, no date, CW: 5 ex. *B. rectangula* (here designated lectotype indicated by a red ring) as *Bimichaelia* on slide K. 172a. at ZSS, Remarks (29).


Norway, Finse, 1200 m, moss, 12 Sept. 1993 MU: 3 ex., U45.


**Unchecked published records.** France and Algeria, in Grandjean (1943) as *B. campylognatha*.

Germany, in Alberti et al. (1981) as *B. campylognatha*.

Ireland, Sphagnum and damp moss, in Halbert (1923) as *B. crassipalpis*; Co. Clare, The Burren, in Evans (1953) 3 ex. as *B. crassipalpis*; Co. Wexford, Carnsore Point, dune edge, in Purvis (1982) as *B. crassipalpis*.

Poland, Glatzer Schneeberg, 1200 m, moss on stone in dry beck, in Willmann (1956) as *B. rectangular*.

Sweden, S- and E-slopes of Säkok, moss and fallen leaves, July 1907, in Trägårds (1910) as *B. setigera var. sarekensis*. 

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Remarks 26. The description of *Bimichaelia sarekensis* is based on fresh material collected by me from the Scandinavian montane area, where the *locus typicus* of *Bimichaelia setigera* var. *sarekensis* is also situated and where no other Bimichaeliini have been found in spite of repeated efforts. Trägårdh (1910: 469) observed only two solenidia on tarsi I, although three solenidia seemed to be a commoner option on the basis of fresh material. However, this is still within the limits of intraspecific variation, as is the case for the number of solenidia - two or three - on tarsi II (Figs. 108, 109). There is also the possibility that Trägårdh missed the third solenidion on tarsus I: its position can be so close to the second solenidion, that they can look like a single solenidion from above, or its position can differ from the line of the other two so that, in lateral view, it is out of simultaneous focus with ω1 and ω2 when observed with a light-microscope.

Remarks 27. The holotype is lost and there are no specimens of the species at NMI (see Material). The synonymization of *B. crassipalpis* is based on two facts: (1) the figures and description by Halbert (1923, Figs. 22a-b): length 320μm; both setae in and dorsal setae branched at the base; pedal setae similar to those of the body; clear reticulation on prodorsal shield and (2) *B. sarekensis* seems not to be infrequent on the eastern coast of Ireland (see Records).

Remarks 28. I have not seen any specimens of the possible syntype series from the Grandjean Collection. The synonymization of *B. campylognatha* is based on the high-quality figures and description given by Grandjean (1943): in addition to the characters listed in Remarks (27) can be noted: curved chelicera; palpal genu and femur incompletely separated; blunt palpal tarsi with free eupathid k'".

Remarks 29. There is no specific name on three labels of the slide K. 172a. However, the slide labelled *Bimichaelia* is the only one (out of a total of four) in the Willmann Collection with the same type of coverglass, labels and sampling code as on the slide labelled *Pachygnathus arhinosus* n. sp., described in the same paper (Willmann, 1953) and from the same area (Admont) as *B. rectangula*. The designated lectotype of *B. rectangula* at ZSS, München was examined by me using a phase-contrast microscope and circled on the slide.

5.5. *Laminamichaelia* gen. nov.

*Michelia* Berlese & Leonardi, 1901: 15, not Berlese, 1884.
*Michelia* Berlese, 1904: 13, not Berlese, 1884.
*Michelia* Berlese, 1910a: 201, not Berlese, 1884.

*Bimichaelia* Grandjean, 1942: 89 and 1943: 1(135), in part (subnuda, arbusculosa and diadema only); Womersley, 1944: 135, in part (australica, novazealandica, pusilla, stellaris and subnuda only); Willmann, 1956: 233; Shiba, 1969: 95, in part (reticulata only); Shiba, 1976: 151, in part (arbusculosa and ramosus only); McDaniel, 1980: 180; McDaniel & Bolen, 1983: 816, not Thor, 1902.

For a complete list of entries, see also under each species.

Type species *Bimichaelia arbusculosa* Grandjean, 1942 from France.

At the moment, sixteen to eighteen species in three species groups are included in this group. The *arbusculosa*-group comprises: *Bimichaelia arbusculosa* Grandjean, 1942 from France and Algeria; *Michelia sylvestrana* Leonardi, 1901 from Chile; *Bimichaelia australica* Womersley, 1944 from South Australia; *Bimichaelia novazealandica* Womersley, 1944 from New Zealand; *Bimichaelia reticulata* Shiba, 1969 from Japan; one undescribed species ‘ful’ from Utah; one undescribed species ‘plu’ from
Western Samoa; two undescribed species ‘taa’ and ‘mau’ from Tahiti; and one undescribed species ‘fur’ from South Africa. The setigera-group comprises: Michaelia setigera Berlese, 1904 from Italy; Bimichaelia diadema sensu Shiba, 1969 from Japan, see Remarks (36); Bimichaelia pusilla Womersley, 1944 from South Australia; Bimichaelia ramosus Shiba, 1976 from Malay Peninsula; and Bimichaelia dimixsetosa McDaniel, 1980 from South Dakota / Bimichaelia dimixsetosa ssp. texana McDaniel & Bolen, 1983 from Texas. The subnuda-group comprises: Bimichaelia subnuda Berlese, 1910, Bimichaelia disetosa McDaniel, 1980 from South Dakota, USA; an undescribed species ‘baa’ from South Africa; and an undescribed species ‘ber’ from Australia.

**Etymology.** The first part of the genus name refers to the presence of lamellae on the secondary pattern, an apomorphic character state common to all members of various species-groups of this genus. Further division of the genus will need to be considered when additional new species have been described and a new analysis accomplished.

**Differential diagnosis.** This genus differs from Bimichaelia by the skin pattern, i.e. by presence of transversely packed lamellae of the secondary pattern (Figs. 115, 125, 135). Instead, the primary pattern may be stellate, i.e. the highly regular polygonal or roundish loops of transversely inserted large lamellae form a rosette around a seta, which in turn is also involved in the other surrounding rosettes (Figs. 121, 125, 131, 135, the lamellae are lined up longitudinally one after another in an undescribed Polynesian sp. ‘mau’) or the large primary lamellae are clumped in groups connected by rows and lines of transverse secondary lamellae i.e. the reticular pattern is missing (Figs. 110, 115). The setae are easily discernible because of several elongated cilia per seta at least on the shoulders and middorsum (Figs. 120, 131, 135). Other character states have been listed in Section 5.3 for Lineage VIII.

**Description.** Small to medium-sized in Europe (Figs. 111, 121, 131, also large species elsewhere); polygonal or roundish cells of primary pattern at least on dorsal side or large lamellae in clumps, secondary pattern by transversely and densely in rows, or more loosely together with granules, inserted small lamellae, at least some of the dorsal setae with several long cilia (Figs. 115, 125, 135); accessory setae on prodorsal area of the European species, either both on soft integument and in-area or only on soft integument or additional setae are missing (Figs. 130, 120, 110, also in the pusilla-ramosus complex some specimens have very few if any additional setae on soft integument); subcapitulum either neotrichous (Grandjean, 1943: 39, Fig. 12E-F) or not (Figs. 112, 124); palpal solenidion inserted on a small protrusion, slightly constricted medially and supported either by one (Fig. 123) or by both eupathids k' and k'' (Fig. 119 and in Grandjean, 1943: 39, Fig. 12A-C); two to four baculiform solenidia, aligned one after another on tarsus I, usually two baculiforms on tibiae I, II and III, thin piliform solenidia more or less obliquely orientated (Figs. 123, 126, 133, 136, 137, 138) or thin solenidia ceratif orm (Figs. 113, 114, 116, 117, 118); larvae holotrichous or neotrichous (Grandjean, 1943: 41, Fig. 13A and 56, Fig. 18A).

As mentioned in Section 5.3, the character states of the species groups introduced in the Key should facilitate identification work, but the non-monophyletic groups are not further defined here. Three species of the European fauna are described here, starting with the one most deviating from the type species.
5.5.1. *Laminamichaelia subnuda* (Berlese, 1910) comb. nov.


*Bimichaelia subnuda*. - Vitzthum, 1929: 57, Unchecked; Vitzthum, 1942: 247, Fig. 252 acc. Berlese; Grandjean, 1943: 18; Schweizer, 1951: 57, Remarks (32); Willmann, 1956: 233, Unchecked and Remarks (33); Uusitalo, 1993: 6, Remarks (34); Bernini et al., 1995: 32.


(Figs. 110-119)

Differential diagnosis. This species can be segregated from the rest of the European species of Bimichaeliini by its small size and pattern of large lamellae and from the other species with non-reticulate dorsal pattern (undescribed so far) by the prominent, button-like naso and the solenidial formula: two baculiform solenidia on tibia II being side by side, abaxial one being smaller.

**Description.** Length 175-220 μm (Fig. 111); dorsal setae of segments C, D, E and F with about ten long and several short cilia basally, cila of the setae of the caudal segments along an elongated centre (Figs. 110, 115); ventral setae with a few long cilia basally (Fig. 112); neither crista nor clear prodorsal shield, integument of sensory area only poorly differentiated, less than ten long cilia basally on prodorsal setae *vi, see, exp* and *in*, filamentous sensilla *ve* densely barbed (Fig. 110); subcapitulum with two pairs of setae (Fig. 112); palpal solenidion supported by both eupathidia (Fig. 119); 6-7 genital setae per valve (Fig. 112); 3-4 anal setae per valve (Fig. 112); solenidial formula as given below: two baculiform solenidia parallel on tibiae I, length of baculiform solenidia on tibiae II less than a half of the segment, knob-like famulus I close to solenidion 02 (Figs. 113, 114, 116, 117, 118).

The only confirmed records of *Laminamichaelia subnuda* are from Tuscany.

**Records.** Italy, Florence, Boboli, 1908 AB: 1 ex. **Holotype** on slide 80/49 at BA, Remarks (30); Siena, Porta San Marco, LH alongside city wall under Robinia, Avena, 26 July 2000 MU: several ex., U359 and in author's collection.

**Unchecked published records.** Czech Republic, in Willmann (1956) as *Bimichaelia subnuda*, Remarks (33).

France, in Grandjean (1943) as *Bimichaelia ? subnuda*, Remarks (31).

Germany, in Vitzthum (1929) as *Bimichaelia subnuda*.


Switzerland, Val Furr/Val del Botsch, 2700 m, moss, 2 ex., in Schweizer (1951) as *Bimichaelia subnuda*, Remarks (32).

Canada, Quebec, woodland humus, in Marshall & Kevan (1964) 170 ex. as ? *B. subnuda*, see also Unchecked of *L. setigera*. 

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Remarks 30. The holotype is badly deteriorated, inside an air-finger, and should be remounted. Dimensions and only 4-5 setae can be observed. There might also be another specimen on the slide.

Remarks 31. Grandjean (1943: 19) reported on adults and tritonymphs of a fourth, small and rarely collected Bimichaeliini from France which he assumed to be \textit{subnuda}. The description, in one sentence, of the dorsal pattern of the specimens (on page 22) agrees well with cuticular structure of \textit{L. subnuda}.

Remarks 32. In the Schweizer Collection, NMB, there is one specimen on a slide N957 labelled \textit{B. subnuda}, but the sampling data and note of size (Stavel-chod, 2750m, Moos, 288×180) rather refer to \textit{B. setigera} in Schweizer (1951) or in Schweizer & Bader (1963), meaning ‘Alpin: Stabel-chod/Val Nügflia, 2750 m, in Pflanzenpolster an Schutthalde, 1 Ex., 288×180 µ’ or ‘Alpen: Nationalpark, Stabelchod, 2750 m, in Pflanzenpolster, 1 Exemplär’, respectively. The solitary specimen on the slide is referable to \textit{B. sarekensis} and recorded here under that species. A slide identified as \textit{B. subnuda} (Val Ftur Val del Botsch, 2700 m, in Moos, 2 Ex., 225×117 µ) as given by Schweizer (1951: 57), is at least temporarily lost (Dr. A. Hänggi, in litt.).

Remarks 33. In the Willmann Collection none of the four slides of \textit{Bimichaelia} has data corresponding to those given for \textit{B. subnuda} by Willmann (1956: 233, Czech Republic, \textit{Cetraria islandica} der Gipfelzone oberhalb des Marchloches. 1375 m).

Remarks 34. The record of \textit{B. subnuda} from Finland by Nordberg (1936) lacks validity and should no longer be taken into account in faunistic work according to Uusitalo (1993).

5.5.2. \textit{Laminamichaelia setigera} (Berlese, 1904) comb. nov.

\textit{Michaelia setigera} Berlese, 1904: 13, Fig. 10., Florence, Italy, rotten \textit{Castanea} wood (for the date of 1904 instead of 1905, see L. van der Hammen, 1959: 7), Records. - Berlese, 1910a: 201; Womersley, 1944: 135; Castagnoli & Pegazzano, 1985: 377, list of specimens at BA.


\textit{Bimichaelia diadema} Grandjean \textit{syn. nov.}. - Grandjean, 1942: 90 and 1943: 19(155), Figs. 16A-D, 17A-D, 18A-D, Material and Unchecked; Baker & Wharton, 1964: 200; Shibata, 1969: 95, Fig. 18A-F, Unchecked and Remarks (36); Daniel, 1971: 384, Fig. 84 after Grandjean; Krantz, 1978: 312, Fig. 57-2 after Grandjean; Krivolotsky \textit{et al.}, 1978: 96, Fig. 302l-m; McDaniell, 1980: 181; Kethley, 1990a: 677; Kethley, 1991: 131; Norton & Kethley, 1994: 177;

\textit{Bimichaelia praecincta} Willmann \textit{syn. nov.}. - Willmann, 1956: 233, Fig. 10, Records.


(Figs. 120-121, 123-129; Fig. 122 an undescribed species from Polynesia) Holotype from Italy, Florence, in BA, examined by me using a phase-contrast microscope.

Differential diagnosis. This species can be segregated from all the other Bimichaeliini species most easily by its having lanceolate setae on the dorsum and on the prodorsal rim (Figs. 120, 121), and an S-shaped solenidion \sigma l on tarsi I (Figs. 123, 127).
**Description.** Length 250-450 μm (Fig. 121); primary pattern comprising rosettes of subpolygonal cells around a seta, mostly flanking, sometimes intermingling with each other, lamellae of secondary pattern almost equal in size, a few middle-sized ones among them, dorsal setae mostly lanceolate with scaly surface, some oligociliate setae among them in midline, many on shoulders, laterally and ventrally (Figs. 120, 121, 125, 129); on prodorsum: a few lanceolate accessory setae in sublinear row along lateral margins, tripartite crista with narrow sidewalks and midline with polygons from small naso to sensory area, sensilla ve simple, one pair of lanceolate setae in (Figs. 120); chelicerae pointed, sublinear, concave groove along paraxial side (Figs. 123, 124); three to four pairs of setae on subcapitulum (Fig. 124); medially constricted palpal solenidion in contact with eupathid k’ apically on a small protrusion, k’ free (Fig. 123); 7-8 genital setae per valve (Fig. 129); 3-6 anal setae per valve; solenidial formula as given below, ω1 on tarsus I S-shaped, bases of two quite large baculiforms on tibiae I one after another (not side by side), small solenidia piliform, abaxial famulus I laterodistal (Figs. 123, 126, 127, 128); larva weakly neotrichous, one pair of accessory setae on every segment (Grandjean, 1943: 56, Fig. 18A).

*Laminamichaelia setigera* is present in a wide variety of habitats, including both coniferous and deciduous forests. The species may be Holarctic: it is widely distributed in Europe and has been collected in Asia.


Italy, Firenze-Cascine, legno castagno, no date AB: 1 ex., holotype on slide 23/9 inside finger-like air bubbles but recognizable, 1 ex. on 23/10, 1 ex. on 23/8 and 1 ex. on 23/11 in poor condition, 1 ex. on 23/7, useful, at BA; Tiarno (Trento), legno marcio, no date AB: 1 ex. on 28/37 sub *Michaelia s.*, in good condition, 1 ex. on 28/38 sub *Michaelia s.* at BA; Firenze, Orto dei Semplici, terricco di castagno, no date AB: 1 ex. on 22/5 as *Michaelia clavigera*, **Remarks (35)**; Carrara, 44°N 11°E, *Fagus-valley*, 22 April 1991 PL: 1 ex., U81; Dolomite, Bergamo, Pian Camuno, Monte Campione, 1000m, decaying wood, 26 June 1995 R. Niemi: 2 ex., U147; Siena, Porta San Marco, LH alongside city wall under *Robinia, Avena*, 24 July 2000 MU: several specimens in author's collection.

Poland, Spieglizer Seefelder, *Sphagnum*, no date Willmann: 1 ex. on slide 65 as *Bimichaelia*. **Lectotype** of *B. praecisca* Willmann, 1956 here designated by a red ring on the slide, at ZSS, cf. Willmann (1956: 233, Fig. 10). The lectotype was examined by me using a phase-contrast microscope.

Russia, Tuva Republic, S-range of Tannu Ola, 50°54’N 94°29’E, Aryskanny-Khem’ River, 5 km ENE of Khol’-Oozha Village, LH *Alnus, Larix, Populus laurifolia*? and *Caragana*, 19 June 1995 MU: 1 ex., U304.

no place, no date, Willmann: 1 ex. as *Bimichaelia* (labels and coverglass similar to slide Lappld.118c, which refers to Abisko, Sweden), at ZSS.

Switzerland, Mtr. Pr. V, Stavel-chod 2750m, Moos 18 July 1930 JS: 1 ex. on slide N957 as *Bimichaelia subnuda*, 288:180, at NMB, see also **Unchecked** of *L. subnuda*. 72

Remarks 35. Schenk et al. (1935: 19) are of the opinion that nomina nuda may often be usefully included in the synonymies, whereas for Mayr (1969: 347) a nomen nudum has no standing in zoological nomenclature and is best never recorded, not even in synonymy, because there is always the danger that such a listing provides an indication in the sense of Chapter 4 of the Code and thus inadvertently makes the manuscript name available - as has happened in this case of Michaelia clavigera. New Acari, which Berlese had under inspection, i.e. identified, named and recorded in his catalogue but never published, are called species in pectore (Castagnoli & Pegazzano 1985). The specimen was examined by me using a phase-contrast microscope and e.g. the S-shaped solenidion φ1 is visible, like on the specimens of B. setigera at BA.

Remarks 36. I have not seen the Japanese specimens and status of Japanese population, recorded as Bimichaelia diadema by Shiba (1968: 219 (2/49)) from Japan; described by Shiba (1969: 95, Fig. 18A-F); and ecologically discussed by Shiba (1976: 98), is unclear. In comparison to the European counterpart, Japanese specimens seem to have: (1) six pairs of subcapitular setae (Shiba, 1969: 96, Fig. 18C) contra four pairs, which may be due to a stronger influence of neotrichy; (2) lancet-like setae more rounded distally (Shiba, 1969: 96, Fig. 18D) contra well-narrowed, but it may be due to the style of drawing; (3) solenidion φ1 on tarsus I straighter (Shiba, 1969: 96, Fig. 18E) contra S-shaped, but the solenidion is drawn from above; (4) 5-7 solenidia on femur I (Shiba, 1969: 96, Figs. 18B and 18E) contra 2-3, but intraspecific variation is unknown and; (5) one male reported (Shiba, 1969: 97), whereas European populations are assumed to be thelytokous (Grandjean, 1943: 51; Kethley, 1991: 131; Norton et al., 1993: 44), but this might be a case of spanandry.

5.5.3. Laminamichaelia arbusculosa (Grandjean, 1943) comb. nov.


Bimichaelia stellaris Womersley syn. nov. - Womersley, 1944: 138, Fig. 2F-G, Records.

Bimichaelia ramosa Mihelčič syn. nov. - Mihelčič, 1956: 19, Fig. 13, description; Mihelčič, 1958: 277, only a detailed type location and habitat, Records. (Figs. 130-139)
A holotype was not designated by Grandjean; see Material and Marshall et al. (1987: 4).

**Differential diagnosis.** This species can be segregated from other species with polygonal primary pattern and a branched pair of anterior sensilla by the clearly less ciliated (30 cilia vs. 60) dorsal setae (Fig. 135), solenidial formula, and position of famulus I close to solenidion o2 (Fig. 133).

**Description.** Length 300-500 μm (Fig. 131); primary pattern comprising stellate rosettes of about 8, often tragonal, cells around a seta and 5-6 setae at the orbit, secondary pattern of densely packed small lamellae in rows inside cells, tens (ca. 30) of cilia per seta (Figs. 130, 131, 135); ca. 10 pairs of additional setae on soft prodorsum, around 6 setae on sclerotized in-area, tripartite crista flanked by narrow sidewalks and a midline with polygons from prominent naso to sensillar area, anterior sensilla ve branched (Figs. 130, 132); palpal solenidion supported by two eupathids (Grandjean, 1943: 39, Fig. 12 A-C); genital setae 8-10 per sclerotized valve, large lamellae longitudinally in rows (Fig. 139); anal setae 4-7 per valve; solenidial formula as given below, 3 and 2 baculiforms on tarsi I and II, respectively, 2 baculiforms side by side on tibiae I, II and III, knob-like famulus I abaxial to solenidion o2 (Figs. 133, 134, 136, 137, 138).

*Laminamichaelia arbusculosa* is restricted to the Mediterranean area in Europe, but the species seems to have dispersed to other continents as well.

**Records.** Italy, Liguria, Savona, Toirano, under stones in macchia, 20 April 1986 PL: 5 exx., U327, U328, 4 ex. in alcohol.

Spain, according to Mihelčič (1958) Jesús del Monte, Santander, Waldregression von Quercetum, Rendsina, dichter Unterwuchs, no date (1955?) WS: 1 ex. (inside a finger-like air bubble) as *Bimichaelia ramosa* n.sp. Mih Sp 355, **holotype** on slide no. 20.02/7560 at MNCN, Mihelčič Collection, examined by me using a phase-contrast microscope.

South Australia, Mount Arden, 12 miles N of Quorn, in moss, Nov 1943 HC: 1 ex. as *Bimichaelia stellaris* n. sp., **holotype** on slide N1952109 at SAM, Womersley Collection, examined by me using a phase-contrast microscope.

**Unchecked published records.** France, in Grandjean (1943) as *Bimichaelia arbusculosa*.

Malaysia, tropical rain forest, in Shiba (1976) 4 females as *Bimichaelia arbusculosa*.

**Remarks 37.** The results of Grandjean’s studies of alycins (*dugesi, denasutus, trichotus, ornithorhynchus, leucogaster*) and Bimichaeliini (*campylognatha, diadema, arbusculosa*) were published in several papers. Comparisons between the species were considered in the first paper of each series (1936 and 1942, respectively). The proper descriptions appeared in the papers published in 1937 for the alycins and in 1943 for the Bimichaeliini. Many characters, some even specific ones, had been listed, however, already in the introductory remarks a year before, and the names of some species were no longer **nomina nuda** but available, in the sense of art. 13.1. of the Code (1999). Yet the dates of the publications with Grandjean’s full descriptions with figures of all the species are followed here consistently.
The observed number of solenidia in European Bimichaeliini on legs I-II-III-IV is as follows:

<table>
<thead>
<tr>
<th>Species</th>
<th>Tarsi</th>
<th>Tibiae</th>
<th>Genua</th>
<th>Femora</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>augestana</em></td>
<td>3B-2B-0-0</td>
<td>1B-1B-1B-1B</td>
<td>3C-3C-1C-1C</td>
<td>2C-1B-0-0</td>
</tr>
<tr>
<td><em>sarekensis</em></td>
<td>2/3B-2/3B-0-0</td>
<td>1B-1B-1B-1B</td>
<td>4C-3C-1C-1C</td>
<td>2C-1B-0-0</td>
</tr>
<tr>
<td><em>subnuda</em></td>
<td>2B-2B-0-0</td>
<td>2B1C-2B-2B-1B</td>
<td>5C-1B2C-1'2C-1C</td>
<td>4C-1C-0-0</td>
</tr>
<tr>
<td><em>setigera</em></td>
<td>2B-2B-0-0</td>
<td>2B1'2P-2B1P-2B-1B</td>
<td>4/5P-1B3P-1B-1P</td>
<td>3P-1B1P-0-0</td>
</tr>
<tr>
<td><em>arbusculosa</em></td>
<td>3B-2B-0-0</td>
<td>2B3P-2B2P-2B-1B</td>
<td>5/6P-1B3P-1P-1P</td>
<td>2'3P-1B-0-0</td>
</tr>
</tbody>
</table>

6. Taxonomy of European Petralycini

6.1. Introduction

Kethley (in Norton et al., 1993: 44) listed *Petralycus* as including 6 species. I have seen specimens from Europe (1 sp.), South Africa (2 spp.) and North America (1 undescribed sp. ‘pet’).

The delineation of the tribe corresponds to the definition of the genus. Yet there are differences, e.g. in the number of fundamental setae between the species. However, because only one European species is known, interspecific relationships are not considered here.

6.2. Petralycini new rank

Tribe Petralycini


Bimichaeliidae Kethley, 1982: 118, in part (*Petralycus* only), erroneous orthography.


Type genus: *Petralycus* Grandjean, 1943

In addition to the synapomorphies listed in Chapter 3.1 petralycins have:
1. Tendency to small size (less than 500 μm in length).
2. Dorsal setae on separate microplates (Fig. 142).
3. Dorsal setae in two rows on C-segment (Figs. 141, 150). A holotrichous European species has the fundamental setae of dorsal segments inserted in more or less transverse rows except for the pairs of c1-c4 (bc-bh) and c2-c3 (bd-bk), which form two clearly separate rows on the C-segment of this primitive petralycin species, whereas a peculiar neotrichy has arisen in the South African petralycins (Theron 1977, Figs. 1, 17).
4. Loss of posterior pair of lateral eyes (i.e. they are eyeless) (Fig. 140).
5. Presence of a pointed naso (Fig. 140). Sharp, tapering naso is unique to the lineage. A more primitive naso is either a broad flap or an eye-like button.
6. Additional lobes on rutellar membrane (Fig. 144). Alycins also have ventral lobes, but presence of several small lobes ventrodistantly on rutella is unique to the lineage. Primitively a rutellum is supposed to be a smooth, tapering seta directed anteriorly. (7. One pair of adorals (Figs. 9, 22 in Theron 1977). This character state, however, is not quite obvious. Tiny and reduced setae are hard to see from old slide material. Grandjean (1943: 6) observed only one seta, which he proposed to be an atavistic remaining of a former adoral seta and, according to Lindquist & Palacios-Vargas (1991), there are no adoral setae in petralycins. Presence should be verified by SEM).

Differential diagnosis. This tribe (and genus) can easily be segregated from the rest of the Endeostigmata by the strongly elongated but robust chelicerae (Fig. 143); two pairs of prodorsal sensilla in separate bothridia, anterior pair ve being globular and posterior pair sci filamentous (Fig. 140); palpal tarsi having a solenidion extending partly over a pair of distal mucronate eupathids (Fig. 145).

Description. Small in size (less than 500 μm); transverse lamellae sparse on integumental ridges, dorsal setae on separate microplates (Fig. 142), setae holotrichous, or neotrichy well developed on middorsal segments, but missing or poorly developed on caudal segments (Fig. 141, and Theron, 1977: 40, 43, Figs. 1, 17); on prodorsum: naso tapering, lateral eyes missing, setae exp missing, anterior pair of sensilla ve globular, posterior pair sci filamentous (Fig. 140); chelate chelicera with five to seven teeth (Fig. 143); pointed rutella with five to seven distal lobes (Fig. 144); palpal solenidion enlarged, reaching over palpal apex, one pair of stiff, acanthoid eupathidia apically on palp (Fig. 145); a pair of supracoxal setae (ep) present on bases of palpi dorsally and a pair of supracoxal setae (el) present on dorsal bases of legs I (not drawn in Figures); first pair of legs remarkably larger that the other legs, tarsi of leg I with only one solenidion (Fig. 146), transformation series of pedal solenidia from claviform and baculiform to uniquely thin, but not tapering (Figs. 147-149).

6.3. Petralycus Grandjean, 1943


(Figs. 140-145, 147 and 150 copied from Grandjean, 1943; Figs. 146 and 148-149 copied from Theron, 1977.)

Type species by original designation: *Petralycus unicornis* Grandjean, 1943 from Périgueux, France.


Differential diagnosis. The genus can be segregated from the other genera of Alycidae and most of the Endeostigmata by the prodorsum with less than six pairs of
fundamental setae (Fig. 140), anterior pair of prodorsal sensilla being globular, and a tapering naso.

**Records.** Republic of South Africa: holotype of *Petralycus longicornis* on slide, PT: holotype of *Petralycus brevicornis* on slide, PT.

USA, South Carolina, 1997 VE LaRoche: 3 ex. at OSU as *Petralycus*.

**Unchecked published records.** France, Périgueux, mineral soil, 19?? FG: several specimens in Grandjean Collection as *Petralycus unicornis*.


6.3.1. *Petralycus unicornis* Grandjean, 1943


(Figs. 140-145, 147 and 150 copied from Grandjean, 1943)

A holotype was not designated by Grandjean, see Material.

**Differential diagnosis.** This species can be segregated from other species of the genus by holotrichous dorsum (Fig. 141) and solenidial formula.

**Description.** Length 280-360 µm (Fig. 141); dorsum holotrichous (Fig. 141); numerous small additional setae on ventral side; on prodorsum: elongated naso tapering and pointed, globular sensilla ve sparsely barbed, filiform sensilla sci ciliated, short setae vi, sce and in sparsely ciliated, eyes and setae exp missing (Fig. 140); elongated cheliceral shafts robust, without cheliceral setae (Fig. 143); pointed rutella with broadly lobed membrane ventrodistally (Fig. 144), no additional setae on subcapitulum; palpal tarsi with enlarged solenidion reaching over two stiff, terminal eupathids (Fig. 145); 11-15 genital setae per valve; 4 anal setae per valve; solenidial formula as below: all solenidia claviform/baculiform (Fig. 147), numerous barbed eupathids ventrally on tarsi I, famulus I laterodistal, famulus II missing.

*Petralycus unicornis* has only been collected once in France from mineral soil.

**Records.** France, Périgueux, Mongaillard, mineral soil, 1941 FG: 1 ex. from syntype series in poor condition at ZMT, U342, see Material.

Observed number of solenidia in the European *Petralycus*:

<table>
<thead>
<tr>
<th>tarsi</th>
<th>tibiae</th>
<th>genua</th>
<th>femora</th>
</tr>
</thead>
<tbody>
<tr>
<td>unicornis</td>
<td>1-1-0-0</td>
<td>4-2-2-2</td>
<td>5-2-2-2</td>
</tr>
</tbody>
</table>

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7. Fossils

Hirst (1923, Figs. XIa, XIb, Text-figs. 1, 1a, 1b, 2) described *Protacarus crani* from silicified strata in Scotland (the Rhynie Chert Bed, Aberdeenshire, UK), presumably peat during the Devonian age about 400 million years ago, and assigned it to the family Eupodidae. Thor and Willmann (1941: 131) consider the species to be a member of Pachygnathidae (Endeostigmata of Grandjean, 1939) owing to the form of: epivertex (=naso); mandibles (=chelicera); palpi; legs; and setae, especially the fan-shaped ones. The flap-like naso, chelate-dentate chelicera, linear palpi and subequal segments of legs are plesiomorphisms that can only be found in Alycini, as well as two claws and a claw-like empodium in all four pairs of legs. However:

1. Fan-shaped setae (in Text-fig. 1b, and probably in Fig. XIb) can only be found in the extant families Nanorchestidae (*Speleorchestes*), Oehserchestidae (*Oehserchestes*) and Grandjeanicidae (*Grandjeanicus*), but members of those families do not have tridactyl pretarsi on the first pair of legs;
2. The setae, as drawn on the legs of the illustrated specimens, seem not to be barbed but rather smooth and more like thorns (Fig. XIb). This is not the case in the extant species of Alycidae;
3. The pattern of ventral setae (Fig. XIa) deviates from that found in Alycidae resembling more the pattern found in Alicorhaghiidae;
4. If the three peg-like processes on the naso (Fig. XIb) are of setal origin as proposed by Hirst (p. 456), this is not a typical character for Alycidae;
5. A pair of long setae at the base of naso could be the pair *vi*, but the four other setae on the left rim of prodorsum that resemble the setae on C-segment cannot be named (Fig. XIb), and their presence seems to exclude the possibility of two pairs of (filamentous) prodorsal sensilla, if the fossil had the primitive number of six pairs of primary prodorsal setae, as is still the case in the Alycidae;
6. No traces of cheliceral setae, eyes, dorso-sagittal setae or solenidia are shown in the Figures;
7. The division of femora of the leg IV is not convincing in Text-fig. 1 (p. 457): starting from tarsus, the first transverse line separates segments as if to mark an immobile joint between tarsus IV and a short tibia IV, which is not the case in Figures XIa and XIb, and Text-fig. 2 shows the tibia IV as being relatively long.

Only the holotype specimen (specimen no. 2, Fig. XIb in Hirst [1923]) was considered to belong to the Pachygnathidae (= Alycidae of this paper) by Dubinin (1962: 464). Yet five of the seven remarks above are presented in the figure of holotype, thus excluding Alycidae as an option.

Dubinin's (1962) division of Hirst's six fossils into five species representing four extant families is subject to criticism (Kethley *et al.*, 1989), if only because it was based solely on Hirst's illustrations. Not only crucial characters like dorsal and prodorsal chaetotaxy, sensilla, solenidia and visual senses are missing from the drawings of the fossils, but those character states that are illustrated, may suffer from the difficulty of studying such tiny fossils.

As Hirst (1923: 457) describes in the text, the pedal setae are usually slightly curved, there seemed to be a long dorsal hair on a tarsus IV, and terminally there are thin hairs on the tarsi shaped like claws. Therefore, judging only from the drawings, it is impossible to determine whether a claw or a claw-like empodium or just a curved seta is
shown. It may even be premature to exclude the family Alicorhagiidae, as proposed by Dubinin (1963), on basis of the curved terminal lines only (Kethley et al., 1989).

The Devonian specimens, deposited at the Natural History Museum in London, should be reexamined using modern research equipment. There are deficiencies either in the remains themselves or in the original interpretation of their morphology. Hence their relationships to extant species remain unresolved at the moment.

Gourret (1888: 437-439, pl. XX Fig. 2) described Pseudopachygnathus maculatus from the Tertiary period and saw some similarities in appearance to Pachygnathus villosus. Yet the figure and description (e.g. length 10 mm) of the species excludes it from Acarina, as was previously noted by Thor and Willmann (1941: 132).

8. Other species included in the Alycidae

Rhyncholophus devius C.L. Koch, 1838

C.L. Koch (1838, vol. 17 nr. 19) described Rhyncholophus devius which he later (C.L. Koch, 1842: 38-39) transferred to the genus Alycus. According to Koch's description, A. devius is very small (?200-300 μm), brownish-yellowish, hairy and, judging from its general appearance, could correspond to any of the species so far included in the Alycidae, given the possibility that the specimen illustrated might represent an immature developmental stage. In fact Berlese (1893: 34) proposed A. devius to be conspecific with Alycus roseus C.L. Koch, 1842. Oudemans (1937: 866) listed devius in the genus Pachygnathus, but on the next page (p. 867) he indicates that devius is conspecific with Bimichaelia augustana Berlese, 1889 (450-700 μm in length). Thor & Willmann (1941: 141) doubted that synonymy because of the difference in size and classified the species as an uncertain Pachygnathus. Since then, Pachygnathus devius has not been mentioned in the literature. The type locality is Nuremberg (Nürnberg), Bavaria where several species of the family can be found. On grounds of its insufficient diagnosis, this species must be considered as a species inquirendae.

Pachygnathus (?) cavernicola Oudemans, 1939

Mégnin (1876: 330) described Gamasus spaeleus without any illustration. Earlier in the article he discussed characters of the gamasides (Mesostigmata) in general and briefly in one sentence (p. 323) remarked larvae of the species have a mixture of T-form setae on dorsal side and branched ones elsewhere. Oudemans (1939: 77) supposed the larvae to belong to the family Pachygnathidae. T-form setae are not rare on larvae of certain families in Parasitiformes (Karg, 1989), but in fact larvae with both types of setae do occure also in Nanorchestes (Niemi et al., 2002), which was commonly thought to belong to the Pachygnathidae (=Alycidae) before 1937 (see Chapter 1.1.3). Oudemans’ interpretation of the larva as belonging to Pachygnathus can be considered as a mistake at least. Such setal types do not exist in Alycidae as currently defined. However, it is beyond the scope of this revision to speculate further on the possible generic identity of this species, especially because the characters mentioned by Oudemans are not even sufficient to identify a family.
Coccalicus clavatus Willmann, 1952

Willmann (1952: 154, Fig. 10 a-d) described Coccalicus clavatus gen. and sp. nov., which he included in the family Pachygnathidae. The type locality is the Island of Wangerooge, Germany and the holotype slide is deposited in the Willmann Collection, ZSS, Munich (München), Germany. No other preparations or specimens of the species exist at the Collection. The slide of the species has been examined by me and Dr H.M. André (Belgium). The solitary specimen with a pair of clublike sensilla is referable to Tydeoidea, which now comprises more than 40 genera. The results of the identification work have been published by André & Uusitalo (2006).

9. Discussion

9.1. Descriptive work

Mayr (1969: 13) cited mites as an example of a poorly known animal group for which a large part of the world fauna will remain unsampled, unnamed and unclassified for decades to come due to a lack of taxonomists. Yet even the published labours of earlier generations can sometimes delay the desired results, especially when the improvement in research methods and equipment has been overwhelming since the pioneering works (still highly considered), as is the case in acarine taxonomy.

The quality of descriptive work has varied greatly. Bearing in mind the subjectivity of character interpretations and the importance of senses, an attempt was made to prepare a standardized and succinct descriptive format for morphospecies:

**Dimensions.** Only length of an observed adult morph(s) is expressed as an indication of size. Males are smaller than females. Intraspecific variation is unknown, and there is a high risk of error, due to distortion of produced either by ballooning or plication of the soft body. Even when sufficient specimens are available, the making of measurements and calculation of statistically significant means with ranges are time-consuming (Usher & Edwards, 1986). Approximate dimensions of organs can be obtained from the Figures, if required.

**Body and Skin.** The importance of the fine morphology becomes evident with SEM. Granulae and glabrous areas, fine and coarse ridges, small and large lamellae, holotrichous and neotrichous areas, microplates or larger sclerotized areas, plumose and simple setae – all must be considered. For segments, see Section 9.2.1.

**Prodorsum.** This is the key area for any diagnostic description. Every prodorsal pattern proved to be specific on closer examination. The creation of a sort of collection of SEM-figures of prodorsal areas considerably accelerated the exploration of the European mite community. For preliminary listing of taxa of an area, checking of the number of various prodorsa seemed to be enough. A remote goal for applied purposes could be an illustrated guidebook of the Endeostigmata or even Prostigmata. Instead of settling for family-level (cf. Chapter 1.1.1.), future students of soil ecology, biodiversity and nature conservation might be able to identify their specimens of this ‘difficult’ group to species using pictorial keys of the prodorsa (cf. Appendix 2). If ‘producing of something useful for wider audience’ is assessed to be a typical phenomenon of ‘good science’ in any field, then such a guide could be considered as a typical end product in taxonomy. For organs and evolution of the prodorsum, see Sections 9.2.2 and 9.2.3.
**Chelicera and Subcapitulum.** Several of anterior setae, including cheliceral and adoral setae, have lost most of their barbs but remain tactile in nature. Rutella have become modified in relation to feeding. All these features proved to be diagnostically important. For the chelicera, see also Section 9.2.4.

**Palpi.** Palpal tarsi with a solenidion and the transformed setae called eupathids in apical position must be described. See also Section 9.2.5.

**Genital and anal areas.** Neotrichous numbers of the setae on valves of both areas are included in the definition of species as a concession to tradition. The neotrichous areas are of minor importance in the taxonomy of Alycidae.

**Legs.** Being setal in origin, solenidia are also subject to neotrichy and therefore their numbers alone are not quite reliable. Yet because they are inserted only on the dorsal side of a segment, they are usually well countable and a valuable addition to the list of sensory organs. Tiny famuli behind the setae and the ventrodistal eupathids are hard to observe by SEM and hence are not systematically reported here. For solenidia, see Section 9.2.1.

Any revision should be based on comparisons of type material, but acquiring fresh material from the type localities or nearby permits even more accurate examination of the key characters. Possible inaccuracies or errors in the early descriptions and pictures can thus be rectified. A comparison between the old outline drawings and new SEM-pictures is easy. Usually the differences lay in smaller details, such as structure of integument and fine morphology in general. Old slide material may be deteriorated and useless, there may be difficulties of accessibility (cf. Grandjean, 1964: 556), or a slide may simply no longer exist. In such cases new material for SEM-work is invaluable. This facilitates the searching and observation of characters, and the possible discovery of new ones, enabling a more versatile comparison of relationships. Micrographs of the organs of interest can easily be taken and sent off electronically and safely, unlike the data from the specimens preserved more traditionally on slides or in alcohol (see Material). Moreover, examination of the tiniest characters is far less frustrating, due to better resolution.

The SEM has its shortcomings. Organs can be damaged in the process. Complete dehydration and a strong electron beam may twist or damage the natural structure (Fig. 74) or delicate constructions, like the cheliceral digits of Bimichaeliinae. The projecting legs with substantial numbers of setae and eupathids are easily charged, and therefore difficult to observe sometimes. The vision may become blurred and exact counting become difficult. Thin recoating by cold may overcome the problem, but as a rule, calculations of the setae have not been attempted here, particularly because neotrichy lessens the value of such information.

Another drawback is that the electron beam is not transilluminating. Although some internal structures, such as teeth of Bimichaeliinae, dorsal surfaces of subcapitulum, eugenital setae, sexual organs and genital papillae are occasionally exposed, the material of the species was too scanty and fragmentary to enable a complete observation of the organs. The shortage of juveniles, the small number of specimens per species, and hence the lack of data on the extensiveness of neotrichy of various organs, all strongly reduced number of potential characters in analysis. Likewise, tiny organs, like famuli or cupules, may be difficult to discover among the ciliated setae (Fig. 99) or complicated surface patterns, and they are only sporadically noticed. The structures may be of minor importance in a taxonomic work like this, but the contrary may be true in studies focusing in more detail on evolutionary questions. Of course, the specimens for examination should also be in a suitable condition: for example, organs covered by debris are usually useless for SEM (Fig. 108).
The routines in preparing specimens for SEM differ and may appear laborious, compared to working on light microscopy. In fact, these small mites are easy to transpose because they adhere to the tip of a micro-needle by static electricity, and an intentionally lateral position permits examination of practically all the essential surface structures. Obscure spaces may indeed remain on the surfaces lying downwards, because the sputtering of gold comes from above, but a stub can be replaced diagonally in the apparatus and recoated. The above difficulties are far outweighed by the possibility to compare three-dimensional pictures, and the higher magnifications possible (due to the much higher resolution), which allows the fine morphology of organs, like eyes and naso (e.g. Figs. 12 vs. 75 and 96) or the structural details of integument, such as lamellae of Alycini and secondary patterns of Bimichaeliinae (e.g. Figs. 10 vs. 95), to be examined in greater detail than with the light microscope.

The importance of the fine morphology in acarine taxonomy also justifies the selecting of a holotype from SEM-material (cf. Pachygnathus wasastjerna). This technique also opens up new perspectives in the interpretation of evolutionary pathways. Knowledge of a complicated case, like the superorder Acariformes, which was still considered as a kind of dump before the summarizing and annotated papers of the assemblage by Kethley (1982, 1990a), continues to be very insufficient, to the point that almost any evolutionary scenario can envisaged at this point. This is discussed below in Section 9.2.

9.2. Of evolutionary processes: comments and speculations with reasoned arguments

9.2.1. Major division of Alycidae

Womersley (1944) divided Alycidae into bimichaeliins and alycins on the basis of cheliceral structures. In addition to the synapomorphies listed in Chapter 3.1 for Lineage V, the evidence of the third main clade comes down to two characters. Firstly, Grandjean (1935), cited also by Norton (1977), proposed an evolution of solenidial structures from the primitive bat-shaped/rod-shaped through thinning, tapering and finally long and pointed. Grandjean called the respective evolutive steps claviform/baculiform, ceratiform, piliform and tactile solenidia, based on the receptor's appearance. The primitive petralycin solenidia, which Grandjean called claviform, are not actually clavate, as are the golf clubs, but rather more like the baseball bats, in form (Fig. 147). Ceratiforms and piliforms are widely distributed among the small solenidia of the bimichaeliins and alycins, whereas only claviform and baculiform solenidia occur in the petralycins, suggesting that the petralycins were segregated from the bimichaeliin and alycin lines before the mutations for thin, evenly to tip tapering models emerged in the solenidial evolution.

Secondly, the present opisthosomal C-segment shows internal muscle attachments as a sign of two archetypal segments which later became fused (van der Hammen 1969). On dorsal side four pairs of setae are inserted in a single row in the holotrichous larvae of alycins and bimichaeliins (Figs. 151, 152, Grandjean, 1943: 56, Fig. 18A), whereas the setae on the C-segment of petralycins are in two rows (Figs. 141, 150), as if the process of segmental fusion remained incomplete as far as the setae are concerned. This again suggests an early separation of the petralycins from the rest of the Alycidae, hence in terms of the Linnean hierarchy, a tribe level seems to be well founded for the
lineage. It also implies that the several reductions, e.g. number of adorals, palpal eupathids, lateral eyes, famulus II and empodial claw, proposed to be shared with bimichaeliins by earlier authors, can instead be interpreted as homoplasies. In other words, the shared apomorphic character states are interpreted as being due to convergence and thus of minor importance to phylogeny.

Ventrally, the contiguous coxisternal shield II of legs III and IV could also be considered as an indication of fusion, and the legs and C-segment as belonging to the same body segment, although this is against two earlier hypotheses of the segmental relations between podosoma and opisthosoma by Grandjean (1970: there is no counterpart of the podosoma on the dorsal side) or Sitnikova (1978: legs III and IV correspond to segments C and D, respectively). Evans (1992) has summarized the theories of acarine segmentation.

The fourth major lineage is monotypic, consisting of an African Bimichaeliinae ‘sil’ (Appendix 3), is based on primitive character states of the prodorsum, chelicera and legs and will be described later.

9.2.2. Evolution of prodorsum

Tergites have also fused in the acarine prodorsal area, anterior to the C-segment. There is a number of ideas related to distribution of original segments, and Kethley (1990a) has interpreted the prostigmatid (=actinedid) prodorsum as representing two to four imperceptibly fused tergites. Grandjean (1970) interpreted the aspidosoma or prodorsal area of actinotrichid (acariform) as being constructed of precheliceral, cheliceral and palpal segments, and this interpretation was followed by most authors, such as Coineau (1974) for Caeculidae, and obviously by van der Hammen for Alycus (1970a: 6, naso represents a precheliceral segment; 1972: 9, possible acceptance of the dorsal reduction of podosomal segments). However, the extent of the reduction in the podosoma is impossible to ascertain on the basis of our present knowledge (Evans, 1992). In an alternative hypothesis, Zachvatkin (1952: 17, Fig. 9) interpreted the prodorsum of Alycus as being composed of the segments of the chelicera, palpi, legs I and legs II. Jesionowska (1991: 265) assumed six segments on an eupodoid prodorsum to be discernible by fragments of ornamentation lines (acron with naso; I and II rudimentary sensory segment with vi and ve + sci, respectively; lateral lips + rutella type segment bearing sce; cheliceral segment with in; and pedipalpal segment with exp). What these different hypotheses have in common is the enumeration of segments from the front backwards and the suggestion that relics of ancient mouthpart segments are incorporated into the prodorsum.

In an attempt to understand prodorsum of these primitive mites, some character states in Figures lead attention to the question of prodorsal evolution in the ancestor of Alycidae. The evolution might be seen differently when moving from mid-dorsum towards the mouthparts:

Fig. 141. C-segment is a composite of two ancestral segments. The holotrichous number of dorsal setae on (next to prodorsum located) C-, D- and E-segments is four, two and two pairs, respectively. Assessment 1: The primitive number of setae on the prodorsal segments is also two pairs.

Fig. 8. In the most primitive character state, the setae beyond the sclerotized sensory area (exp and sce) are inserted above the two pairs of lateral eyes as if the eyes had eyebrows. Assessment 2: The mecanoreceptors and the visual senses may belong to two different segments.
Fig. 8. The pair of setae, $vi$, is inserted above the naso, which is considered to represent a reduced pair of eyes (Grandjean 1943, Kethley 1990a). Assessment 3: Setae $vi$ and naso may be two elements of the third segment.

Fig. 8. On the sclerotized sensory area, there are two pairs of sensilla ($sci$ and $ve$) and one pair of setae ($in$). In several prostigmatic families the sensilla have transformed into setae. Assessment 4: Setae $in$ were originally sensilla but have been reduced to setae.

Fig. 25. The most proximal organs on prodorsum are the posterior pair of (lensless) eyes, the smallest pair of setae ($exp$) above the eyes and the pair of setae ($in$) on midprodorsal sclerite. Assessment 5: The organs are reduced and they are members of the same ancient segment.

Fig. 25. The reduced proximal organs have counterparts of normal form in front of them (the anterior pair of lateral eyes, the pair of setae $sce$ above the eye lenses and the pair of sensilla $sci$ on the sclerite). Assessment 6: The ‘normal’ organs belong to another ancient segment.

Figs. 150 vs. 151. The fusion of two ancient segments into the C-segment is accompanied by a fusion of the rows of dorsal organs (setae), i.e. the setae of the posterior segment move forwards into same row as the setae of the anterior segment. Assessment 7: The fusion of setae into one row is not yet completed in the petralycins.

Figs. 25 vs 150. The proximal organs are as closely inserted to their anterior counterparts (lateral eyes, $exp$-$sce$, $in$-$sci$) as are the incompletely fused setae on C-segment of petralycins. Assessment 8: The proximal organs have moved onwards in the fusion of prodorsal elements of two ancestral segments.

Figs. 150 and 140. On petralycin C-segment, the space between counterparts of the anterior pair of setae $bc$ (= $c1$) is small compared to the space between the counterparts of setae $bd$ (= $c2$), whereas in the corresponding situation on prodorsum, the counterparts of the anterior pair ($sci$) are far from each other and the counterparts of setae $in$ lie between the sensilla $sci$. Assessment 9: The counterparts of sensilla $sci$ have moved wider apart from each other.

Figs 8 vs. 52. The smallest pair of setae ($exp$) in primitive species is inserted above the reduced pair of lateral eyes, but in advanced species they are above the eye lenses of the anterior pair of lateral eyes. Correspondingly the pair of setae $sce$ is inserted above the eye lenses in primitive species, but well anteriorly in more advanced species. Assessment 10: The setae have moved forwards along the lateral margins of the prodorsal sclerite.

Figs. 8 vs. 25 vs. 82. The nasal area may gradually disappear and eventually the counterparts of setae $vi$ become frontal and very close to each other. Assessment 11: There is a reduction process going on in the anterior part of prodorsum. By going backwards in time then, the naso is replaced by the anterior pair of eyes, and secondly each eye with $vi$ has moved into their present position from more lateral place. In other words, escorted by the pair of setae $vi$, the eyes have moved along the margin of sclerite into anterior position, reduced into naso and finally disappeared. Grandjean (1943: 25 and Fig. 14B) speculated also the possibility of the originally three pairs of eyes in the Acari and noted that the alycid median eye is in fact a double eye. Alberti et al. (1991: 346) urge to investigate ultrastructure of eyes to test the homology with the eyes of other Arachnida or Chelicerata.

Fig. 8. In addition to the reduced organs and their counterparts, still on prodorsum, there is the set of sensilla $ve$ on the sclerite, a pair of setae $vi$, and a frontal naso representing a reduced pair of (lateral) eyes. Assessment 12: These organs may belong to the third segment still recognisable on prodorsum. The course of the cleavage
line below the naso in juvenile stages (δ in Fig. 47) supports the naso being a part of this ancient segment.

To summarize the assessments, yet another tritergal option, which deviates from the earlier hypotheses and incorporates the ventral parts in a simple way, could be introduced for the segmental composition of the prodorsum on basis of the genera at hand, if we look at the prodorsum starting from the proximal end instead (cf. Figs. 8 or 25 with 153):

Primitively on the prodorsum, there are three pairs of setae, two pairs of lateral eyes and a frontal naso bearing a pair of eyes on its ventral side. The incomplete fusion of the setae of the petralycin C-segment again suggests there were two pairs of setal organs on each archetypal segment. If we hypothesize that a pair of middorsal sensilla, a pair of lateral eyes and a pair of mechanoreceptive setae above the eyes were inserted on each archaic segment, then traces of only three segments (II, III, IV) can be observed dorsally and the evolution of the present alycid prodorsum could be explained by three processes of movements and reductions.

(1) When segment IV moved forward, it became partially fused with segment III, so that two pairs of lateral eyes now are side by side (again, cf. Alberti et al. (1991) for the homology or homoplasy with the lateral eyes of the other Chelicerata) and, correspondingly, the rows of in–exp and sci–sce are placed near each other, but still forming two separate although somewhat curved rows.

(2) On segment III, sensilla sci drifted apart towards the eyes (growing nerve ganglia underneath?) while setae sce made room by slight anterior movement.

(3) Lateral movement forwards was strongest in the anterior segment II, to create a cone-like frontal part of prodorsum, so that the rows now are curved forward - the frontal pair of eyes, with the escorting setae vi, even meeting at the prodorsal apex.

(4) Reductions took place in the elements of the posterior segment IV. The ancient sensilla transformed into the pair of setae in, setae exp became the smallest ones in size, and the eyes became vestigial. In the anterior segment II, the frontal eyes transformed into naso.

(5) According to this hypothesis the most drastic arching resulted mesal adnation of the appendages of the first (I) segment, but the chelicerae have specialized so early in the evolution for uptake of food that all the other traces of the segmental past have disappeared, except for the strongly modified appendages, the chelicerae themselves.

(6) On ventral side an adduction of the coxae of palpi, legs I and legs II, comparable to the approaching movement on the prodorsal area, can be observed (Fig. 112). The appendages also are strongly orientated forwards and their incorporation into the prodorsal segments could be considered. The first pair of legs dominates vital sensory functions with the aid of high number of eupathids, solenidia and famuli, and so does the corresponding prodorsal area (III), equipped with the sensilla sci and eyes. Restricted importance of the posterior segment (IV) is reflected not only in the reduction of the prodorsal elements, but also in the lower number of sensory organs on the second pair of legs. Still ventrally, the palpi of the anterior segment (II) only focus on searching of food, the rest of the segment being fused into the subcapitulum (Weigmann, 1996), and the frontal eyes have lost their role on the dorsal side.

It is beyond the scope of this revision to attend to any extensive comparison or discussion of the various other hypotheses. Kethley (1990a) emphasizes that an assessment of the homologues of the prodorsal setae throughout prostigmatic mites is based strictly on topographic equivalence. However, his setal designations clearly suggests that, instead of longitudinal thinking (cf. ro-exa-exp), the setae should be linked
transversely, i.e. the prodorsal elements should be seen as segmentally linked. The model also suggests a suppression policy of the setae. It appears that the sagittal organs stay longest, or in other words, the loss of organs starts with the lateral ones.

9.2.3. Prodorsal sensilla

As for the prodorsal setae, if the prevailing state of two pairs of trichobothria is accepted as early derivative (Kethley, 1982: 117; Lindquist & Palacios-Vargas, 1991: 353) and the tritergal hypothesis is correct, then implicitly, the trichobothria must be the pairs ve and sci, whereas the condition vi as being trichobothrial along with sci is more derived, as prevails in at least Sphaerolichidae and seven prostigmatic families (for listing, see Kethley, 1990a: 751). This view is supported by the strong tendency to the regression of the organs of segment IV, i.e. the loss of posterior eyes, the loss of setae exp, as well as the transformation of an ancient pair of trichobothridia to ordinary setae in and, finally, to the loss of setae in (Petralycus brevicornis Theron, 1977).

The cases of petralycins, bimichaeliins and alycins, however, represent their own ancient states in the fusion of prodorsal elements. In more advanced groups of mites, such as Oribatida and Astigmata, where fusion of the segment IV to the segment III has become complete, the pair of setae in between the sensilla sci seems to grow in size and undoubtedly regains something of its old significance, while the setae exp, if present, can still be recognized as being the smallest pair.

The uniform symbols for the setae by Kethley (1990a) are approximately in line with what this new hypothesis indicates concerning the original positions of the prodorsal organs on the archaic segments, except that, logically, setae vi and ve should have their names reversed. However, Kethley’s notation is strictly followed in this work to avoid any confusion. Nor is the proposal by van der Hammen (1969) of the homology of the prodorsal setae of actinedids and oribatids followed in the setal notations of modern literature (Norton, 1990). In the traditional system for Astigmata (Philips, 1990, Fig. 22.1), sci should be in of Kethley’s system, and the setal nomenclature of dorsal setae again does not reflect segmental thinking.

In any event, as long as the hypotheses are based on morphology without ontogenetic additions, the hypothesis presented here will, like any other proposed for the segmental relationship of prodorsal seta, remain arguable and invite scepticism, especially in regard to the most derivative groups of mites with highly complicated prodorsal transformations.

9.2.4. Chelicera

Elongation of chelicera independently four times is in accordance with the view of this work: twice by retaining their robustness, obviously as a response to edaphic conditions, in both the Petralycus and the Amphialycus; twice by transformation into narrow beaks, but, perhaps, for different reasons: in the Pachygnathus for living and feeding in moist environments, and in the Bimichaeliini as an adaptation to feeding on plants or mycorrhizae (Prof. D.E. Walter, in litt.).

Lindquist (1999) proposes a possible relationship between Eriophyoidea with styliform mouthparts and Pachygnathoidea. For example, he refers to edentation of the
bimichaeliin chelicera and the styliform rutella of *Pachygnathus s.s.t.* adopted from the figures by Grandjean (1937C, Fig. 8; 1943, Figs. 5, 14).

In spite of the diminution of the *Pachygnathus*-chelicera, there are tiny teeth on the edges of the digits (Figs. 3, 63) which well correspond with the dental projections of the other alycins and petralycins (Figs. 2, 143), and there is also a trend to a diminution of the rutella. The problem is that the detailed structure of the cheliceral teeth (Fig. 8D) and rutellar lobes cannot be properly seen by the magnifications used by Grandjean. Although drawn in the Figure 8C, which presents gnathosomal structures in lateral position, the rutella rather resemble those observed from above (Fig. 52). In fact, by observing from the lateral side the rutellum is like a miniaturized hand (Fig. 58, 66), and not a pointed and specifically elongated precursor of a stylet, as Grandjean’s commentary and figures erroneously suggest.

No longitudinal dentition, present on the outer edges of the cheliceral digits of the petralycins and alycins, is present in the Bimichaeliinae group (Fig. 14B) either. Instead, a rake-like serration on the inner surfaces of the digits of at least some Bimichaeliinae (Fig. 122 and Grandjean, 1943: 38) is present, but difficult to observe due to its position. The outer edges of the bimichaeliin chelicera are smooth, but the number of internally inserted ‘teeth’ may be high, very variable in size (anterior ones are smallest), and they are arranged obliquely in the line. The serration obviously differs from the teeth of the petralycin and alycin lineages in terms of use but they may be homologous in origin.

Lindquist’s idea of a sequence of structural modifications from *Petralycus* through *Pachygnathus* to *Bimichaelia* is based on partly imperfect information. The phylogenetic results of this work (Fig. 1) do not support his idea either. This does not, however and self-evidently, exclude the possibility of the eriophyid-type chelicera from being evolved of an ancestor with chelate-dentate chelicera as proposed by Lindquist (1999) because the chelate-dentate form is primitive for mites.

### 9.2.5. Palpi

According to the results presented here, the evolution among the Alycini leads from six pseudacanthoid eupathids in the *Alycus*, through a number of five or four in the *Pachygnathus* and the subgenus *Amphialycus* (*Amphialycus*), to the basally fused group of four eupathids, as in the subgenus *Amphialycus* (*Orthacarus*). One pair of TP-type eupathids of the Bimichaeliinae and one pair of mucronate eupathids of the Petralycini are independently evolved in number and form. Perhaps the two missing pairs are lost during ontogeny. The palpal tarsus is reduced in size so that originally a small alycin-type solenidion with dorsoproximal insertion now partly reaches over terminal eupathids in the Petralycini, and is dislocated into apical position in the Bimichaeliinae.

### 9.2.6. Cladistic trees

Morphology-based cladograms have been prepared to determine relationships between Alycidae and other taxa of Acariformes and Endeostigmata since O'Connor (1984). The subsequent hypotheses have treated structure of Sarcoptiformes (Lindquist & Palacios-Vargas, 1991), Trombidiformes (Lindquist, 1999) or both (Norton et al., 1989). Kethley (1989: 215) remarked that there are serious problems in attempts to hypothesize character state polarities because of the lack of an acceptable outgroup to the
Acariformes for assigning polarity. Endeostigmatid families, such as Pachygnathidae, Terpnacaridae and Alicorhagiidae, and non-mite arachnid outgroups, such as Opiliones and Palpigradi, have been used (O'Connor, 1984, Lindquist, 1984). Some amount of uncertainty is evident in the polarities (e.g. presence of empodium vs. median claw, O'Connor, 1984 vs. Lindquist & Palacios-Vargas, 1991, see Chapter 3.1, Lineage VI). Kethley (1991: 134) assumed that outgroup selection within Acariformes is not acceptable (but see Nixon & Carpenter, 1993 and Chapter 2.3), and more distantly related outgroups increase the probability of independent derivation of the character states (O'Connor, 1984), as do the early derivation of the groups involved (e.g. Minelli, 1993), which may be worth noting here because the groups in question date back to the Palaeozoic era.

According to the present analysis, the tribes Petralycini, Bimichaeliini and Alycini should be examined separately. Theoretically then, the members of Alycidae might belong to either the line Trombidiformes, which includes Prostigmata, or to Sarcoptiformes, which includes Oribatida. This ancient paradigm of a dichotomy of the acariform mites, dating back to the Finnish scientist Reuter (1909), would again demand a broader view and rechecking of all the families, presently acknowledged as the acariforms, by modern methods.

Presently the alycins, bimichaeliins and petralycins are placed as a basal group in the lineage Sarcoptiformes, for which O'Connor's tree (1984) gives three reasons. Some counter arguments can be put forward on the basis of the results from Alycidae:

1. **Tarsus IV without solenidia.** The presence or absence of solenidia on a segment does not necessarily reveal any remarkable remoteness or closeness in relationship, at least within the neotrichous taxa like Alycidae. Solenidia are missing on telofemora IV of Alycus denasutus, perhaps of a French population of *Pachygnathus ornithorhynchus (=villosus) sensu* Grandjean (1937c), of all the members of Amphialycus, and on genu III of *Amphialycus oblongus*, but present on those segments of all the other members of the tribe. Also, there is a solenidion present both on tibia IV and basifemora IV of *Alycus marinus* but missing on the segments of the other alycins. There are no solenidia on femora II and IV of the African petralycins, unlike on those segments of *Petralycus unicornis*. Members of *Bimichaelia (s.st.)* are without a baculiform solenidion on genu II, but the other species of the tribe have one and the solenidial number of right and left may differ on *Bimichaelia sarekensis*. The number of solenidia in these cases, perhaps, rather tells about variation in the intensity of neotrichy, as also Grandjean proposed for *Sphaerolichus barbarus* (1939: 102) and for *Lordalycus peraltus* (1939: 119). Both species have neotrichous legs with solenidia on tarsus IV, and are now included in Trombidiformes.

2. **Prodorsum differentiated but unsclerotized.** Softness of an integument is hypothesized to be within the ancient state than hardness. As a rule, the appendages (chelicera, palpi and legs), genital valves and prodorsal sensory area are sclerotized in Alycidae. O'Connor (1984) postulates a transformation series from soft to a highly sclerotized prodorsal integument. Even if it is presumed that prodorsal sclerotization of the early derivative mites is in its initial phases, comparison between the alycin and bimichaeliin prodorsa suggests lumping of these two types into the same category is unfounded (cf. Figs. 8 vs. 100).

In the alycin-type sclerotization, vast areas of prodorsum from the pair of setae in up to the nose are hardened, whereas primitive Bimichaeliinae, such as *Bimichaelia*, are without any prominent sclerosis of the prodorsum, which again suggests an independent hardening of the sensillar area in the advanced Bimichaeliini (Fig. 130). The prodorsal sclerite of the petralycins rather resembles that of alycins. In general, choice
between homology and homoplasy of the prodorsal shields is problematic. There must have been a high selection pressure to have some sort of hardening around the sensilla to stabilize the area, and hence such a modification may have arisen more than once. The hardening process was probably initiated several times in the early epochs and the presence of prodorsal shield alone cannot be considered as a reliable synapomorphy for separate clusters without concern of a sclerite’s form.

**3) Rutellum of a simple shaft with teeth.** According to O'Connor (1984: 128) the sister group Trombidiformes retains the ancestral character state of a setiform rutellum or the derived condition of its complete loss. The interpretation of the rutellum as a hypertrophied seta on the lateral sides of subcapitulum is also adopted here (Grandjean, 1957: 253, but see also Jesionowska, 1991: 277). Bimichaeliinae lacks rutella. For some reason then, this primitively a pointer-like sounding apparatus has been lost by the ancestors of Trombidiformes and the Bimichaeliinae.

Walter (1988) emphasized that feeding habits of Bimichaeliinae are unknown although his qualified opinion was that fluid feeding, or perhaps filtering of fluids seems to be the likely mood of feeding in bimichaeliins. The endeostigmatids with rutella might be ancestors to saprophagous and mycophagous oribatids *sensu* Norton (1985). Bernini (1986: 279) proposed the basic actinotrichid lineages had phytophagous or saprophagous by feeding habits. Furthermore, the South African Alycini with rutella and chelate-dentate chelicera were supposed to feed on fungi by Theron (1979: 577).

The presence of rutella, however, does not necessarily reveal the feeding habits. Walter (1988) found *Alycus roseus* to be a voracious predator feeding on nematodes, citing also *Pachygnathus "marinus"* to be a predator of copepods and tardigrades in a coastal habitat in Europe after Schuster (1979, see also Remarks 15). The stiff rutella is proposed to have a role in cutting of fungal mycelia among oribatids and alicorhagiids by Grandjean (1957) and Theron (1979). The multilobate rutella of the alycins might be used in slicing of nematodes as well, but a membranous structure would rather suggest some other function, e.g. in dental cleansing, especially for the forked type of *Pachygnathus (s.st.)*. The number of membranous lobes corresponds to the dental number of cheliceral fixed digits on the alycins. A similar but multilobate membrane, holding on well to the higher number of teeth on fixed digits, is developed in the petralycins. The adoption of very basic, even predichotomian position for the alycids (before dichotomy of Acariformes into Trombidiformes and Sarcoptiformes) in the tree would suggest a predatory ancestry, common to Acariformes (Actinotrichida) and Chelicerata in general.

Among the proposed synapomorphies for Trombidiformes, setal and segmental losses have been used. Segments may be difficult to discern and are easily lost in Alycidae (*A. trichotus*, Bimichaeliinae) hence the reductions should, perhaps, be considered as tenuous character states, as is the case for neotrichy.

Kethley (1989) recommended a detailed reexamination of the previous hypotheses of relationships, and I share the view that the trees should rather be completely reconsidered. Prior to the tree construction, however, it will be necessary to prepare pertinent descriptions of the twenty or so species of Alycidae from other continents (mentioned in passing above), to check the real nature of the nominal species of the rest of the endeostigmatid families, and to review the applicability of the criteria used in the prostigmatid taxonomy. The use of SEM is by no means a new innovation in the taxonomy of mites (e.g. Woolley, 1970, Griffiths et al., 1971), but it should still provide a powerful tool for these tasks.
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Figures 2-152

Figs. 2-7: Typical chelicera and ventral sides of alycid genera.

Figs. 8-12: *Alycus roseus* C.L. Koch
8.-Prodorsum, microplates of setae vi inseparably linked to sclerotized crista from downwards-bent naso to sensillar area. 9.-Dorsal habitus, pattern of fragmentary ridges. 10.-Integument, lamellae of various size transversely on ridges and a setal microplate. 11.-Genu IV (1 solenidion) and Telofemur IV (1 solenidion). 12.-Eye area, seta sce apart from glabrous lens of anterior eye, while seta exp next to reduced posterior eye.

Figs. 13-24: *Alycus roseus* C.L. Koch
13.-Chelicerae, seta with one basal barb. 14.-Cheliceral digits, seta smooth. 15.-Cheliceral seta with two barbs. 16.-Rutellum with dorso-distal process (arrow) and ventral membrane, lateral lip with three adoral setae. 17.-Rutellum without dorso-distal process (arrow) and without ventral membrane. 18.-Six pseudacanthoid palpal eupathids. 19.-Seta from PS-segment with elongated shaft. 20.-Tarsus I, redrawn from Grandjean (1937a, Fig. 3). 21.-Tarsus I and loss of solenidion /g5502. 22.-Tarsus I and loss of a seta. 23.-Tarsus I with an extra seta. 24.-Forked famulus II. 7-12, 23-24 from Finland, Kuusamo and 15 from Iniö; 14, 17 from Sweden, Tärna; 16, 18-19, 21-22 from Norway, Finse; 20 from France.

Figs. 25-29: *Alycus denasutus* (Grandjean) comb. and stat. nov.
25.-Prodorsum without naso, setae vi on separate microplates far apart. 26.-Dorsolateral habitus, ridges continuous. 27.-Integument, lamellae of various size transversely on ridges, setal microplates. 28.-Genu IV (1 solenidion) and Telofemur IV (no solenidion). 29.-Frontal view of gnathosoma: chelicera, tripartite labrum, unpaired underlip, a pair of lateral lips and rutella.

Figs. 30-35: *Alycus denasutus* (Grandjean) comb. and stat. nov.
30.-Cheliceral teeth and smooth cheliceral seta. 31.-Two claws with barbed shafts and a claw-like, oligosetulate empodium. 32.-Barbed famulus II. 33.-Rutellum without dorso-distal process but with ventral process on ventral membrane (arrows). 34.-Rutellum without dorso-distal process and ventral process (arrows). 35.-Rutellum with dorso-distal process and without ventral process on ventral membrane (arrows). 25-34 from Italy, Toscana; 35 from USA, South Carolina.

Figs. 36-46: *Alycus trichotus* (Grandjean) comb. nov.
36.-Prodorsum with pubescent setae vi and in, setae exp above anterior eye lenses. 37.-Dorsum with heavy neotrichy. 38.-Integument, lamellae of various size transversely on ridges and setal microplates. 39.-Palpal eupathids: two pairs of pseudacanthoids on sides, an acanthoid and a pseudacanthoid with a long cilium in the middle. 40.-Neotrichous larva.

Figs. 41-46: *Alycus trichotus* (Grandjean) comb. nov.
41.-Chelicera, anterior cheliceral seta smooth. 42.-Cheliceral setae, anterior one barbed. 43.-Cheliceral setae, anterior one barbed. 44.-Rutellum with dorso-distal process (arrow). 45.-Rutellum without dorso-distal process (arrow). 46.-Two adoral setae, abaxial one with a long cilium. 36-46 from Italy, Siena.

Figs. 47-51: *Alycus marinus* (Schuster) comb. nov.
47.-Prodorsum of a nymph: dehiscence line 6, elongated vi, anterior eye lenses missing, setae swollen. 48.-Chelicera redrawn from Schuster (1958, Fig. 9). 49.-Rutellum, adoral setae and subcapitular setae. 50.-Palpus with six pseudacanthoid eupathids. 51.-Tibia I (6 solenidia) with two swollen solenidia (arrows), Genu I (6 solenidia) and Femur I (4 solenidia). 47-51 from France, near Marseille.

Figs. 52-56: *Pachygnathus villosus* Dugès [in Oken]
52.-Prodorsum, microplates of setae vi inseparably linked to sclerotized crista, in-area with one pair of setae. 53.-Dorsum, ridges slightly undulating. 54.-Integument, organization of lamellae per size classes weak. 55.-Palpal tarsus with 4 eupathids. 56.-Tibia I (3 solenidia), Genu I (2 solenidia) and Femur I (2 solenidia).

Figs. 57-59: *Pachygnathus villosus* Dugès [in Oken]
57.-Cheliceral digits. 58.-Hand-like rutellum and two adoral setae. 59.-Genu IV (1 solenidion), Telofemur IV (1 solenidion) and Basifemur IV (no solenidia). 52-59 from Italy, Carrara.

Figs. 60-64: *Pachygnathus wasastjernae* sp. nov.
60.-Prodorsum, setae vi on separate microplates, in-area with two pairs of setae (arrows). 61.-Dorsum, ridges strongly undulating. 62.-Integument, organization of lamellae per size classes strong. 63.-Chelicera and palpal tarsus with 5 eupathids. 64.-Tibia I (3 solenidia), Genu I (3 solenidia) and Femur I (5 solenidia).

Figs. 65-67: *Pachygnathus wasastjernae* sp. nov.
65.-Two claws with barbed shafts and a claw-like, oligosetulate empodium. 66.-Hand-like rutellum. 67.-Genu I (3. solenidion) and Femur I (7 solenidia). 60-67 from Finland, Vaasa.

Figs. 68-70: *Amphialycus (Amphialycus) pentophthalmus* Zachvatkin
68.-Prodorsum with eye-like naso. 69.-Palpal tarsus with four eupathids. 70.-Rutellum and one adoral seta. 68-70 from the Ukraine, Harkova, copied from Zachvatkin (1949).

Figs. 71-75: *Amphialycus (Amphialycus) leugocaster* (Grandjean)
71.-Prodorsum with prominent, broad naso. 72.-Dorsum with continuous, slightly winding ridges. 73.-Integument, lamellae subequal in size. 74.-Chelicera (artificially wrinkled), blunt rutellum with distal lobes. 75.-Eye area with finely striated lens of anterior eye.

Figs. 76-81: *Amphialycus (Amphialycus) leugocaster* (Grandjean)
76.-Seta vi. 77.-Palpal tarsus with four barbed eupathids. 78.-Palpal tarsus with five barbed eupathids. 79.-Blunt rutellum and two adoral setae, abaxial one vestigial. 80.-Tarsus I, solenidion o2 anterior to lyrifissure. 81.-Two claws with barbed shafts, a claw-like multisetulate empodium and famulus II with distal barbs. 71-75 and 80-81 from Austria, Salzburg; 76-79 from Bruc a. d. Mur.

Figs. 82-86: *Amphialycus (Orthacarus) oblongus* (Halbert) comb. nov.
82.-Prodorsum without naso, setae vi on prodorsal sclerite close to each other, supracoxal setae ep and el present. 83.-Dorsal habitus. 84.-Integument, lamellae subequal in size. 85.-Palpal tarsus with four barbed and fused eupathids. 86.-End view of a nymph with caudal anus.

Figs. 87-89: *Amphialycus (Orthacarus) oblongus* (Halbert) comb. nov.
87.-Famulus II with distal barbs. 88.-Tarsus I with solenidion o2 anterior to lyrifissure. 89.-Tarsus I with solenidion o2 at abaxial end of lyrifissure. 82-89 from Italy, Toscana.

Figs. 90-94. *Bimichaelia augustana* (Berlese)
90.-Prodorsum: six pairs of setae and cristal area from naso to sensilla weakly reticulate. 91.-Habitus, with multisetoceous genital area, bidactyl legs and undivided femora IV. 92.-Palpus with separate genu and femur, subcapitulum without rutella and adoral setae, cf. Fig. 97. 93.-Tibia I (1B=1 baculiform solenidion) and Genu I (3C=3 ceratiform solenidia). 94.-Barbed basis of flagelliform sensillum ve.

Figs. 95-99. *Bimichaelia augustana* (Berlese)
95.-Integument of C-segment: reticular primary pattern (roundish areoles) of large lamellae, secondary pattern granular, setae with a long cillum and a few short barbs. 96.-Striated naso. 97.-Palpal solenidion with supporting eupathid k', k" free (arrows). 98.-Tarsus I (3B), Tibia I (1B) and Tarsus II (2B). 99.-Frontal view of Tarsus I with two barbed claws and multisetulate, clawless empodium, focused on Famulus I (arrow). 90-99 from Italy, Treviso.
Figs. 100-104. *Bimichaelia sarekensis* Trägårdh
100.-Prodorsum: six pairs of setae and cristal area reticulate. 101.-Habitus with roundish areoles. 102.-Palpus with partially fused genu and femur (arrows point to joint), chelicera bent. 103.-Tibia I (1B) and Genu I (4C). 104.-Capitate sensillum *sci* with barbs, the form typical to all bimichaeliines.

Figs. 105-109. *Bimichaelia sarekensis* Trägårdh
105.-Integument of C-segment: reticular primary pattern (roundish areoles), granular secondary pattern and setae with a long cilium and a few barbs of which 2-3 elongated. 106.-Striated naso and seta vi. 107.-Genital valves with 6-7 genital setae. 108.-Right tarsus II (3B, arrows). 109.-Left tarsus II (2B, arrows) of the same specimen as in Fig. 108. 100-109 from Norway, Finse.

Figs. 110-114. *Laminamichaelia subnuda* (Berlese) comb. nov.
110.-Prodorsum, with six pairs of setae. 111.-Dorsal habitus, without reticulate primary pattern. 112.-Ventral habitus, weakly developed neotrichy and 6-7 genital setae per valve. 113.-Tarsus I (2B) with Famulus I (arrow). 114.-Tibia I (2B side by side [arrows also in Fig. 113], 1C), Genu I (5C) and distal part of Femur I (3C of 4C on frame).

Figs. 115-119. *Laminamichaelia subnuda* (Berlese) comb. nov.
115.-Integument of clearly segmented caudal segments F-H-PS: primary pattern of clumps of large lamellae, secondary pattern of granules and small lamellae, elongated setae with several cilia of various length and without microplates. 116.-Tarsus II (2B), Tibia II (2B side by side, arrows), Genu II (1B2C) and Femur II (1C). 117.-Tibia III (2B side by side, arrows), Genu III (1C). 118.-Tibia IV (1B), Genu IV (1C). 119.-Frontal view of palpal tarsus, solenidion supported by both eupathids (arrows). 110-119 from Italy, Siena.

Figs. 120-124. *Laminamichaelia setigera* (Berlese) comb. nov.
120.-Prodorsum: tripartite crista, neotrichous rim of soft integument, no additional setae on sclerotized *in*-area. 121.-Dorsum: substellate primary pattern, lanceolate setae mostly, a few ciliate setae in midline (arrows also in Fig. 120) and on flanks. 122.-Chelicera of an undescribed *Bimichaeliini* sp. 'mau' from Tahiti. Row of obliquely inserted 'teeth' (14 or 15) of various size classes on inner edge of movable digit. Outer edge is smooth. 123.-Chelicera beak-like, palpal tarsus with apical solenidion and a free eupathid (arrow), Tarsus I (2B, o1 S-shaped, cf. Fig. 127), Tibia I (2B1P= two baculiform solenidia and one piliform solenidion on right Ti or 2P on left Ti), Genu I (4P), Tarsus II (2B), Tibia II (2B1P). 124.-Non-neotrichous subcapitulum, inner surfaces of chelicera with an excavated groove, forming a tube when appressed to each other.

Figs. 125-129. *Laminamichaelia arbusculosa* (Grandjean) comb. nov.
125.-Dorsal integument of D-segment with two kinds of setae: ciliate ones and lanceolate ones with scaly barbs, primary pattern polygonal, secondary pattern of even rows of small lamellae. 126.-Tibia III (2B), Genu III (1B). 127.-Position of knob-like Famulus I (arrow). 128.-Tibia IV (1B), Genu IV (1P). 129.-Genital valves: large lamellae transversely in rows, 7-8 genital setae per valve. 120-121, 123 and 125-129 from Italy, Toscana; 124 from Finland, Kangasala.

Figs. 130-134. *Laminamichaelia arbusculosa* (Grandjean) comb. nov.
130.-Prodorsum: crista, both soft integument and *in*-area neotrichous. 131.-Dorsum with regular stellate pattern. 132.-Roundish naso, setae vi, and tripartite crista. 133.-Tarsus I (3B) and Famulus I (arrow), Tibia I (2B side by side (arrows) and only 1P of 3P on frame). 134.-Tarsus II (2B) with eupathids ventrodistally (arrows).

Figs. 135-139. *Laminamichaelia arbusculosa* (Grandjean) comb. nov.
135.-Dorsal integument with multiciliate setae, primary pattern polygonal, secondary pattern of even rows of small lamellae. 136.-Tibia I (2B side by side [arrows], 3P), Genu I (6P), Femur I (3P). 137.-Tibia II (2B side by side [arrows], 2P), Genu II (1B3P), Femur II (1B). 138.-Tibia III (2B side by side, arrows), Genu III (1P). 139.-Genital valves: large lamellae longitudinally in rows, 8-9 genital setae per valve. 130-139 from Italy, Liguria.

Figs. 140-149. *Petralycus* 140.-Prodorsum: eyes missing, five pairs of setae (setae *exp* missing), anterior pair of sensilla capitata, sparsely barbed. 141.-Dorsal habitus, holotrichy, setae on C-segment in two rows. 142.-Integument, lamellae sparsely inserted on ridges, setal microplate. 143.-Chelicera elongated but robust. 144.-Rutellum pointed with lobed membrane. 145.-Palpal tarsus, a pair of mucronate eupathids distally, dorsal solenidion swollen, reaching over the
tip. 146.-Leg I twice the size of leg II. 147.-Claviform solenidia on first tibia, genu and femur of *P. unicornis*. 148.-Claviform/baculiform solenidia (with constricted basis) on Tibia I, Genu I and Femur I of *P. longicornis*. 149.-Thinned but non-tapering solenidia (not ceratiform/piliform) of Tibia I, Genu I and Femur I of *P. brevicornis*. 140-145, 147 from France, Périgueux and copied from Grandjean (1943); 146, 148-149 from RSA and copied from Theron (1977).

Figs. 150-153. 150.-*Petralycus* larva: dorsal setae homomorphic, ciliated, in two rows on C-segment, filamentous sensilla *sci* ciliated, non-swollen, sensilla *ve* capitate. 151.-*Bimichaelia* larva: setae basally ciliated, c1, c2, c4 in a row, c3 (bk) slightly anteriorly, sensilla *sci* capitate, filamentous sensilla *ve* sparsely barbed. 152.-*Alycus* larva from Finland, Kuusamo: setae with elongated shafts, basally more densely ciliated, c1-c4 in one row, sensilla ciliated, slightly swollen. 153.-A hypothesis: Three prodorsal segments (II, III, IV) of hypothetical archetype with middorsal sensilla (*in, sci, ve*) and mechanoreceptoral setae (*exp, sce, vi*) above eyes transforming into present form and position of prodorsal elements, see Chapters 9.2.2. and 9.2.3. and cf. e.g. Fig. 8. Figs. 150-151 from France, Périgueux and copied from Grandjean (1943).
Appendix 1. Character states used in defining Alycidae by earlier authors

A brief history of some characteristics and character states proposed since 1885 for definition of a joint-category for alycins, bimichaeliins, and from 1942-on also for petralycins.

1. Body (9)-segmented: Berlese 1885, 1893; G. Canestrini 1891; Vitzthum 1929, 1943; Grandjean 1937d; Thor & Willmann 1941;
2. Sejugal furrow present: G. Canestrini 1891; Hull 1920; Thor & Willmann 1941; Baker & Wharton 1964;
3. Integument soft (i.e. weakly sclerotized), extendable: G. Canestrini 1891; Trouessart 1892; Berlese 1893; Oudemans 1904; Vitzthum 1943; Baker & Wharton 1964; Krantz 1978;
4. Setae finely ciliated: Thor & Willmann 1941;
5. Six pairs of setae on prodorsum: Grandjean 1937d;
6. Two pairs of well developed sensilla present in large pores (bothridia): Hull 1920; Vitzthum 1943; Grandjean 1937d; Womersley 1944; Baker & Wharton 1964; Krantz 1978; Kethley 1990a; Thor & Willmann 1941;
7. Anterior pair of prodorsal trichobothria inserted normally on prodorsum (not on naso, not set in a common depression): Kethley 1990a;
8. Naso present: Berlese 1893, 1899; Trägårdh 1910; Thor & Willmann 1941; Womersley 1944; Baker & Wharton 1964;
9. Prodorsal shield present: Thor & Willmann 1941; Womersley 1944;
10. Peritremes absent: Kethley 1990a;
11. Labrum unsclerotized: Kethley 1990a;
12. Chelicera chelate-dentate: Berlese 1885, 1893, 1899; G. Canestrini 1891; Trouessart 1892; Oudemans 1904; Trägårdh 1910; Vitzthum 1929, 1943; Grandjean 1937d; Thor & Willmann 1941; Baker & Wharton 1964; Krantz 1978;
13. Fixed cheliceral digit normally produced (i.e. not truncate): Krantz 1978; Kethley 1990a;
14. Palpi simple (i.e. without a clawlike seta): Berlese 1885, 1899; G. Canestrini 1891; Vitzthum 1929, 1943; Baker & Wharton 1964; Kethley 1990a;
15. Genital opening a longitudinal slit: Berlese 1893; Thor & Willmann 1941;
16. Three pairs of genital discs/acetabula (conforming to Oudemans' rule): Berlese 1893; Vitzthum 1943; Grandjean 1937d; Thor & Willmann 1941; Baker & Wharton 1964; Krantz 1978;
17. Rutella present: Krantz 1978; Grandjean 1937d; Thor & Willmann 1941; Womersley 1944; Baker & Wharton 1964; Krantz 1978; Kethley 1990a;
18. Protective scale of larval organ present: Grandjean 1937d.

The following characteristics have also been proposed, although the character states are absent in at least one of the tribes (1) Alycini, (2) Petralycini or (3) Bimichaeliini:
- One or two eyes on prodorsum: G. Canestrini 1891; Trouessart 1892; Berlese 1893; absent in (2) and (3).
- Three pairs of adoral setae: Grandjean 1937; absent in (2) and (3).
- Cheliceral setae present (1 or 2): Thor & Willmann 1941; Krantz 1978; absent in (2) and (3).
- Rutella present: Krantz 1978; absent in (3).
Appendix 2. Selected figures of prodorsa for comparison
Appendix 3. Selected figures of an undescribed species ’sil’ from South Africa: prodorsum, chelicera and legs.