

ON SOME PROBLEMS IN THE SYSTEMATICS OF FEATHER MITES

О НЕКОТОРЫХ ПРОБЛЕМАХ В СИСТЕМАТИКЕ ПЕРЬЕВЫХ КЛЕЩЕЙ

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Key words: feather mites, taxonomic system, phylogeny, idiosomal chaetotaxy, homology of chaetome
Ключевые слова: перьевые клещи, таксономическая система, филогения, хетотаксия идиосомы, гомология хетома

ABSTRACT

Two problems in the systematics of feather mites are discussed. The first problem concerns the macrosystematics of feather mites, their taxonomic frames, arrangement of recently recognized families into superfamilies, and phylogenetic relationships among their superfamilies. Two general concepts in regard to the taxonomic frame and taxonomic system of feather mites recently exist. The concept of Gaud and Atyeo [1996] is most detailed and widely used in practice by taxonomists and other investigators of the group in question, while the concept of O'Connor [1982a] most adequately reflects the phylogenetic relationships between higher taxa of feather mites. The second important problem in the study of feather mite concerns the homology of the ventral hysterosomal setae (coxogenital setae) among different taxa of feather mites, and, respectively, the assignation of chaetotactic nomenclature to them. Several hypotheses of homology of the ventral hysterosomal setae in different taxonomic groups of feather mites are proposed and discussed.

РЕЗЮМЕ

Работа посвящена обсуждению двух проблем в систематике перьевых клещей. Первая связана с определением таксономических рамок для этой экологической группировки астигматических клещей, объединением выделяемых в настоящее время семейств в надсемейства и родственными связями высших таксонов перьевых клещей. В настоящее время существует две основные таксономические системы перьевых клещей. Система Го и Этио [Gaud, Atyeo, 1996] наиболее детализирована и широко используется на практике систематиками и другими исследователями этой группы, тогда как система О'Коннора [O'Connor, 1982a] более адекватно

отражает филогенетические отношения между высшими таксонами перьевых клещей. Вторая проблема заключается в установлении гомологии вентральных гистеросомальных щетинок (коккальных и генитальных) как между различными таксономическими группами перьевых клещей. Предложено несколько гипотез и обсуждается их применимость в отношении тех или иных таксономических группировок перьевых клещей.

INTRODUCTION

Feather mites are a vast group of astigmatid mites that are permanent parasites or symbiotes of birds, and live on their plumage or skin [Dubinin, 1951, Peterson, 1975; Gaud, Atyeo, 1982a, 1996; O'Connor 1982a, 1982b; Mironov, 1999; Dabert, Mironov, 1999; Proctor, Owen, 2000; Proctor 2003]. This group currently includes over 2400 species (in 450 genera, 33–36 families, 3 superfamilies) distributed throughout the World and occurring on almost all recent orders of Aves, with the exception of penguins (Sphenisciformes). As it is very popular to stress in general papers on feather mites, this number of feather species is estimated by experts to be less than 20% of possibly existent species. In general appearance, feather mites are rather typical astigmatid mites with body size ranging from 300 to 700 μm , and with relatively well sclerotized tegument in comparison to free-living Astigmata. They are highly specialized and occupy discrete microhabitats on the bodies of birds. For instance, these mites inhabit feathers only of certain type, and only certain microareas within a fan of such feathers. Experts still disagree whether feather mites should be referred to as parasites or commensals. Some

feather mites that inhabit the skin or quills and feed respectively on the skin tissues and internal corneous parts of feathers are obvious parasites according to all definitions of parasitism. Most feather mites feed on a secretion produced by the oil gland, which birds disperse over their plumage, and usually do not cause any visible damage to the host; therefore, investigators were led to believe that most feather mites are commensals. However, there are enough records that prove that under certain conditions such normally commensal species cause depluming itch and other diseases of birds [Shaw, 1966, Alwar et al., 1958; Alwar, 1970, Oba et al., 1978, Rosen et al., 1988]. Therefore, the feather mites that cause no visible damage to their hosts may be considered to be potential parasites.

Since the discovery of feather mites, the studies of this group have been mainly focused on the investigation of their biodiversity and improving their taxonomic system. Ecological, physiological and anatomy investigations are still extremely rare, apparently because they require rather complicated techniques for rearing in experiments or observations in natural conditions [For references on ecological studies see: Gaede, Knülle, 1987; Kim, 1989; Gaud, Atyeo, 1996; Mironov, 2000]. Phylogenetic studies of this group are also in the stage of naissance. Dubinin [1951] proposed the first phylogenetic scheme of feather mites in the beginning of 1950's, but only a few phylogenetic reconstructions of several feather mite taxa have been carried out since [Mironov, 1991a, 1991b; Dabert, Mironov, 1999; Mironov, Dabert, 1999; Dabert, Ehrnsberger, 1995, 1998; Dabert et al., 2001; Ehrnsberger et al, 2001].

In spite of the extensive study of feather mites begun in the mid-20th century and the significant progress in the elaboration of their taxonomic system achieved by the end of this century, a number of problems concerning the systematics of this group still remain. The present discussion does not intend to list and discuss all essential problems in the systematics of feather mites, but focuses on two of them, which seem to be most important at this point. It also does not propose any final resolutions, because solving these problems requires complex and long-term investigations. The main goal is to point out these problems, propose possible hypothesis and stimulate studies to solve them. In addition, this discussion would be helpful to the researchers, who begins or will begin to investigate feather mites in the near future, to understand recent conceptions in this field and avoid errors.

DISCUSSION

1. Macrosystem of feather mites

The first problem may be expressed as “What are feather mites in systematic and phylogenetic terms?” Of particular interest are the relationships of their highest taxa to each other and to other astigmatids. It is worthy to point out that the scientific definition of “feather mites” (Federmilben — Gm., Acariens plumicoles — Fr.) always directly depended on the dominating taxonomic concept in regard to this group. To illustrate this and also show the historical development of the taxonomic system of feather mites, it is expedient to trace the history of the systematics of this group. Gaud and Atyeo [1996] proposed the first attempt to recognize and determine periods in feather mite studies, but the present paper proposes slightly different subdivisions and other titles for the periods.

Primary period. The first feather mite was mentioned in the “Systema Nature” [Linnaeus, 1758]; it was “*Acarus passerinus* Linnaeus, 1758” from the chaffinch *Fringilla coelebs* Linnaeus. Interestingly enough as a curious, the second feather mites species known up that moment, “*Pediculus pari* Linnaeus, 1758” from the big tit *Parus major* Linnaeus, was placed in that issue among the lice Anoplura, i.e. among insects, not mites. Sixty years later, Nitzsch [1818] established the first feather mite genus *Analges* Nitzsch 1818, which united all feather mites known in that time. The period since the first discovery of feather mites until the late 1860's may be referred to as the primary period of investigation or the period of primary accumulation of biodiversity data.

Classical period. Robin [1868a, 1868b] for the first time used the term Avicular Sarcoptidae, or Sarcoptides avicoles, a suprageneric taxon uniting 5 feather mite genera. Several years later, Robin and Megnin [1877] substituted Robin's term for the term Sarcoptides plumicoles, and proposed the first taxonomic system with detailed morphological characteristics of 5 genera recognized. Further, Trouessart and Megnin [1884a–1884c] treating Sarcoptides plumicoles as a subfamily within the ectoparasitic mite family Sarcoptidae Murray, 1877 proposed an arrangement of feather mite genera into three sections. From 1884 to 1916, Trouessart with coauthors and in monographic papers contributed significantly to the systematics of feather mites and to knowledge of their biodiversity. The final version of his taxonomic system for this group [Trouessart, 1916] included four sections in the subfamily:

Analgesae — 12 genera
 Pterolichoae — 35 genera
 Proctophylloideae — 9 genera
 Epidermopteae — 6 genera

Period of dispersion. In the taxonomic system of Acari proposed by Oudemans [1906a, 1906b], the term “feather mites” did not correspond to any monophyletic taxon of astigmatids. Feather mites (in all modern senses) were represented in his system by 12 families scattered among three different cohorts of Astigmata, together with other astigmatid families represented by free-living forms and parasitic mites on mammals and insects. This artificial Oudemans’ system, in which the higher taxa (the cohorts) were based on convergent morphological characters, was criticized by many contemporary acarologists, and this system was in certain extent an obstacle for a successful development of the systematics of Acari. Nevertheless, this system was used in various modifications by many subsequent acarologists till the end of 1940’s, including experts who dealt with feather mites. For detailed critique of the Oudemans’ system in regard to its influence on the systematics of feather mites — see Dubinin [1953] and Gaud and Atyeo [1996].

Renaissance of feather mites. In the early 1950’s two different authors almost simultaneously had made an attempt to restore feather mites as a monophyletic taxon. The Radford’s attempt [1953] was not much successful, because the proposed system only formally listed all known taxa and did not include any morphological diagnostic bases. In practice, this author had returned to Trouessart’s system [Trouessart, 1916] on the “higher level”. In the classification of Radford, suprageneric taxa of Trouessart (sections) had been raised up to the familial rank and the general familial content had been enlarged by the addition of several families established by Oudemans. Besides, included feather mite families were not formally united under any higher ranking taxon.

Dubinin [1953] had restored feather mites as a monophyletic taxon, the superfamily Analgoidea, encompassing 5 families: Analgidae, Epidermoptidae, Freyanidae, Proctophylloidae, and Pterolichidae. It is possible to stress a Dubinin’s precedence in this idea, because the first volume of his monograph dedicated to feather mites of the USSR [Dubinin, 1951] already contained the suprageneric name “Analgesoidea”, used for all feather mites. Besides, all suprageneric taxa recognized by Dubinin [1953] were provided with

detailed morphological characteristics. The restoration of feather mites as a single taxon and the publication of a three-volume taxonomic monograph in a series “Fauna of the USSR” [Dubinin, 1951, 1953, 1956] catapulted a push for extensive study of feather mites in the World, especially in Europe and Africa [for almost exhaustive bibliographic references see — Gaud, Atyeo, 1996, specifically for European countries see — Mironov, 1996, 1997]. Dubinin’s system [1953] was used successfully over the next 25 years.

Modern period. Up until the late 1970’s, due to extensive biodiversity and taxonomic studies, the number of known feather mite species has increased about 3 times in a comparison to 650 species counted by Dubinin [1953]; the number of recognized genera has exceeded 400, and a total of 30 families existed. This huge collection of suprageneric taxa badly needed some order. The arrangement of families into some groupings (i.e. taxa of higher rank) was necessary in order to form any clear understanding of their relationships. Atyeo [1979] has found that the structure of praetarsi and tarsal chaetotaxy successfully characterize the high ranking taxa of astigmatid mites, such as families and superfamilies. Based on these characteristics (the setting and structure of sclerites in praetarsus; the presence or absence of proral tarsal setae *p*, *q*), Gaud and Atyeo [1978] proposed a new taxonomic system of feather mites, in which 33 families were arranged into 3 superfamilies: Analgoidea, Freyanoidea, and Pterolichoidea. The creation of this system may be considered as a starting point of the modern period of the study of feather mites. The latest version of this system [Gaud, Atyeo, 1996] is shown in the Fig. 1. Several years later, based on the same characteristics as Gaud and Atyeo [1978] used, O’Connor [1982a] proposed another taxonomic concept in regard to feather mites. His taxonomic system included a wider range of families treated as feather mites and demonstrated rather different arrangement of families into superfamilies (Fig. 1).

Thus, there are two different high-level taxonomic systems of feather mites in today’s acarological literature. In regard to defining certain astigmatid families as feather mites, the system of Gaud and Atyeo [1978, 1996] may be referred to as a “restricted concept” and O’Connor’s [1982a] as a “wide concept.” The main arguments presented by these authors for arranging the families into superfamilies may be briefly described as follows.

In the frame of the supercohort Psoroptidia, the main characteristics of the superfamily Analgo-

Family	Gaud, Atyeo, 1996	O'Connor, 1982a
Pterolichidae Trouessart et Megnin, 1884	PTEROLICHOIDEA	PTEROLICHOIDEA
Ochrolichidae Gaud et Atyeo, 1978		
Gabuciniidae Gaud et Atyeo, 1975		
Falculiferidae Oudemans, 1908		
Eustathiidae Oudemans, 1905		
Crypturoptidae Gaud, Atyeo et Berla, 1972		
Thoracosathesidae Gaud et Mouchet, 1959		
Rectijanuidae Gaud, 1961		
Cheylabididae Gaud, 1983*		
Ascouracaridae Gaud et Atyeo, 1976*		
Syringobiidae Trouessart, 1896		
Ptiloxenidae Gaud, 1982*		
Kiwilichidae Dabert, 1994*		
Oconnoriidae Gaud, Atyeo et Klompen, 1989*		
Kramerellidae Gaud et Mouchet, 1967		
Freyanidae Dubinin, 1953	FREYANOIDEA	
Vexillariidae Gaud et Mouchet, 1959		
Caudiferidae Gaud et Atyeo, 1978		
Turbinoptidae Fain, 1957		PYROGLYPHOIDEA
Pyroglyphidae Cunliffe, 1958		
Ptyssalgidae Atyeo et Gaud, 1979	ANALGOIDEA	ANALGOIDEA
Analgidae Trouessart et Megnin, 1884		
Psoroptoididae Gaud et Atyeo, 1982		
Dermoglyphidae Megnin et Trouessart, 1884		
Gaudoglyphidae Bruce et Johnston, 1976**		
Xolalgidae Dubinin, 1953		
Alloptidae Gaud, 1957		
Thysanocercidae Atyeo et Peterson, 1972*		
Trouessartiidae Gaud, 1957		
Proctophyllodidae Trouessart et Megnin, 1884		
Avenzoariidae Oudemans, 1905		
Pteronyssidae Oudemans, 1941*		
Apionacaridae Gaud et Atyeo, 1977		
Dermationidae Fain, 1965*		
Epidermoptidae Trouessart, 1892		
Knemidocoptidae Dubinin, 1953		
Laminosioptidae Vitzthum, 1931		
Cytoditidae Oudemans, 1908		

Fig 1. Arrangement of feather families into superfamilies according to different authors.

* taxa were established or risen up to the familial rank later 1982.

** considered by O'Connor [1982a] as a synonym of Dermoglyphidae.

idea pointed out by Gaud and Atyeo [1978; 1996] are as follows: the presence of the condylophore guide (U-shaped sclerite surrounding distal ends of condylophores) in the ambulacral disc, moderately

elongated and usually thin zigzag-shaped condylophores, and the absence of tarsal setae *p*, *q* (Fig. 2 e–g). The two other superfamilies are characterized by the absence of condylophore guide and

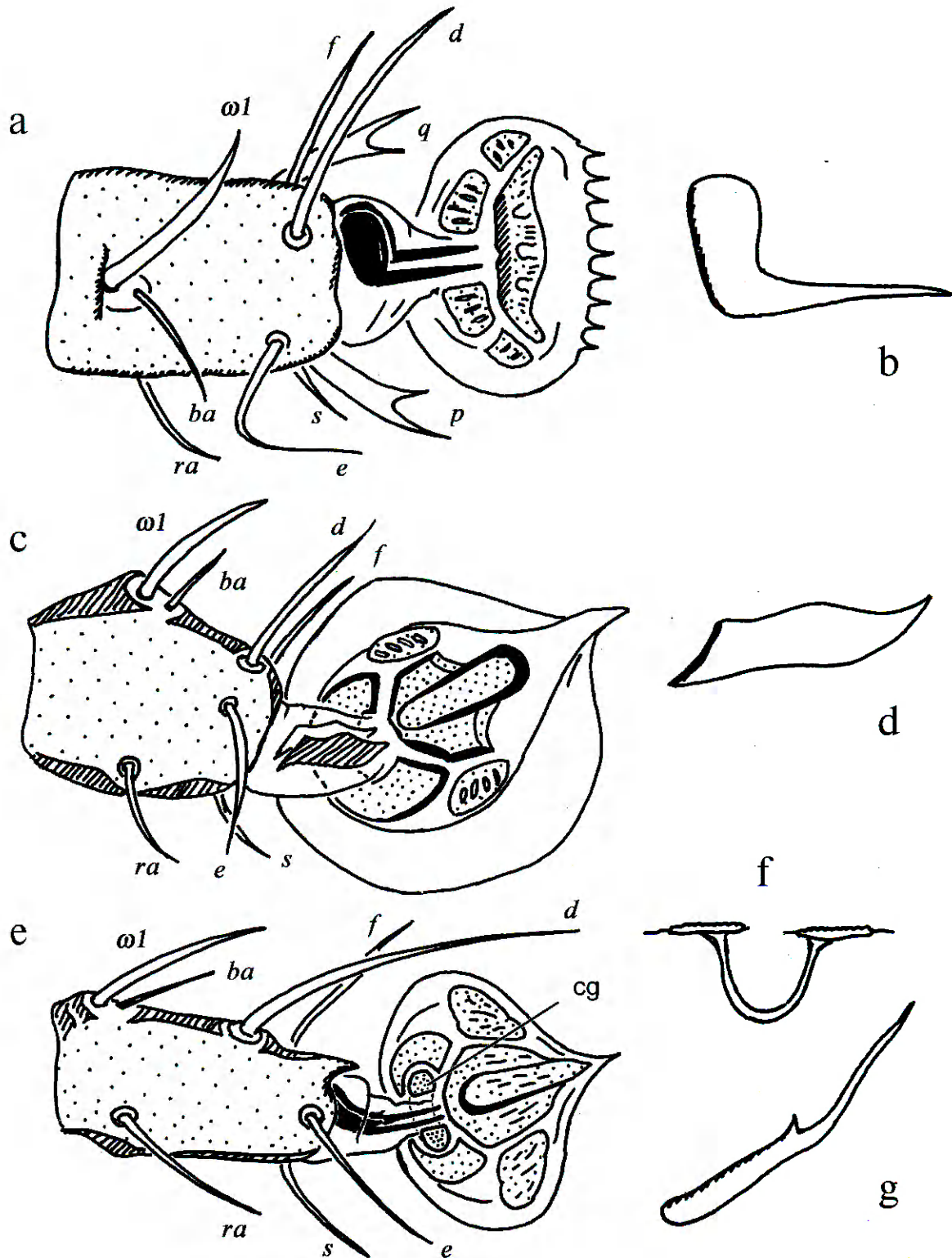


Fig. 2. Schemes of tarsi in feather mites of different superfamilies.

a — *Pseudolichus solutofurtus* (Dubinin) (Pterolichoidea, Pterolichidae), right tarsus II, b — same, condylophore, c — *Freyana anatina* (Koch) (Freyanoidea, Freyanidae), right tarsus II, d — same, condylophore, e — *Bdellorhynchus polymorphus* Trouessart (Analgoidea, Avenzoariidae), f — same, condylophore guide (cg), g — same — condylophore.

relatively short condylophores. In turn, in Pterolichoidea, the condylophores are L-shaped and the proral tarsal setae *p*, *q*, are always present and

flattened, usually leaf-like or bifurcate (Fig. 2 a, b); in Freyanoidea, the condylophores resemble small plates with tapering anterior ends, the setae *p*, *q* are

absent (Fig. 2 c, d). In ecological terms, the system of Gaud and Atyeo includes almost exclusively feather mites located on the plumage or in quills, with the exception of three families: Dermationidae, Epidermoptidae and Pyroglyphidae, representatives of which live on the skin of birds.

According to O'Connor [1982a] the listed characteristics have another taxonomic value for the systematics of Astigmata. He considered that the absence of setae *p*, *q* in Freyanoidea is a less valuable characteristic in the taxonomic sense than the structure of the praetarsi, and included the all three freyanoid families in Pterolichoidea (Fig. 1). This concept seems to be quite reasonable. Further detailed investigation of freyanoid mite morphology in the frame of cladistic study [Ehrnsberger et al., 2001] has shown that many representatives of the family Freyanidae do retain the rudimentary setae *p*, *q* on all legs or on the two hind pairs. As for the structure of condylophores, it is rather easy to imagine, the plate-like condylophores of freyanoid mites could have easily evolved from the L-shaped ones of pterolichooids as the result of abbreviation the thick basal part and a great reduction of the thin distal part.

O'Connor [1982a] significantly enlarged the familial contents of the superfamily Analgoidea to include three families, the representatives of which are not feather mites in the direct ecological sense. Among them, only some representatives of Laminosioptidae really inhabit feather parts: mites of the subfamily Fainocoptinae are located on the external walls of quills and therefore have received the name "quill-wall mites", while Laminosioptinae are intraskin parasites and live in quill follicles. (In my opinion, the subfamily Fainocoptinae should be elevated to the familial rank, but this is out of the scope of the present paper). Mites of the family Knemidocoptidae that cause a widely known disease of birds referred to as "scaly legs," or knemidocoptosis, live in the corneous layer of the skin and under the scales of legs [Fain, Elsen, 1967]. In general appearance, these mites closely resemble scabies mites Sarcoptidae, parasites that inhabit various groups of mammals, but this superficial resemblance is obviously convergent. Close relationships of Knemidocoptidae with skin-inhabiting feather mites, such as Epidermoptidae, was originally pointed out by Dubinin [1953], and this concept was further supported by a cladistic analysis of Analgoidea [Dabert, Mironov, 1999]. The third family Cytoditidae includes parasites that live in the respiratory passages, nasal cavities, lungs

and air sacs of birds. Affinity of this family characterized by degeneration of many structures to feather mites is questionable, but according to O'Connor [1982a], "its placement in the Analgoidea seems preferable to other choice".

Besides, in the frame of supercohort Psoroptidia (Astigmata), O'Connor [1982a] created a new superfamily, Pyroglyphoidea, which included mites with different mode of life, both permanent parasites of birds and free-living forms. The family Pyroglyphoidea, forming a core of Pyroflyphoidea and currently including about 50 species in 19 genera [Gaud, 1968; Fain, Gaud, 1984; Fain et al., 1988; Fain, Atyeo, 1990], unites mites with quite different modes of life. A broad spectrum of life modes exists among these mites: free-living forms (*Dermatophagoides* Bogdanov, 1864), nidicolous forms often having phoretic associations with birds (*Hirstia* Hull, 1931; *Sturnophagoides* Fain, 1967), permanent dwellers of the external surface of plumage (*Asiopyroglyphus* Fain et Atyeo, 1990; *Onychalges* Gaud et Mouchet, 1959), and true quill inhabitants (*Paralgopsis* Gaud et Mouchet, 1959). Mites of the monotypic family Ptyssaligidae live inside quills [Aty eo, Gaud, 1979]. The familial status of the latter taxon as a separate family raises some doubts. Possibly, this taxon represents only a more highly derived lineage of Pyroglyphidae. The third family, Turbinoptidae, consists of mites that live in the nasal cavities of birds [Fain, 1977]. Thus, the family Turbinoptidae is the last in an evolutionary spectrum of living forms within the superfamily Pyroglyphoidea, ranging from commensals to true parasites, i.e. including free-living mites that originally dwelled in nests and eventually evolved into permanent inhabitants of the external parts of plumage, then into quill-inhabiting mites, and finally into cavity parasites.

Two main concepts regarding the family Pyroglyphidae exist: either these mites demonstrate the evolution of Psoroptidia toward parasitism, (the most widely accepted point of view) or, conversely, toward a free-living habit [Gaud 1968, Wharton, 1976; Fain et al., 1988, Gaud Atyeo, 1996, O'Connor, 1982a]. This spectrum of recent living forms observed within the whole superfamily Pyroglyphoidea may be considered to be a model of the development of permanent parasitism in the ancestors of feather mites [Mironov, 1999; Dabert, Mironov, 1999]. Perhaps all major lineages of feather mites (superfamilies) have undergone a similar pathway, which has finally led to permanent parasitism in diverse microhabitats on the

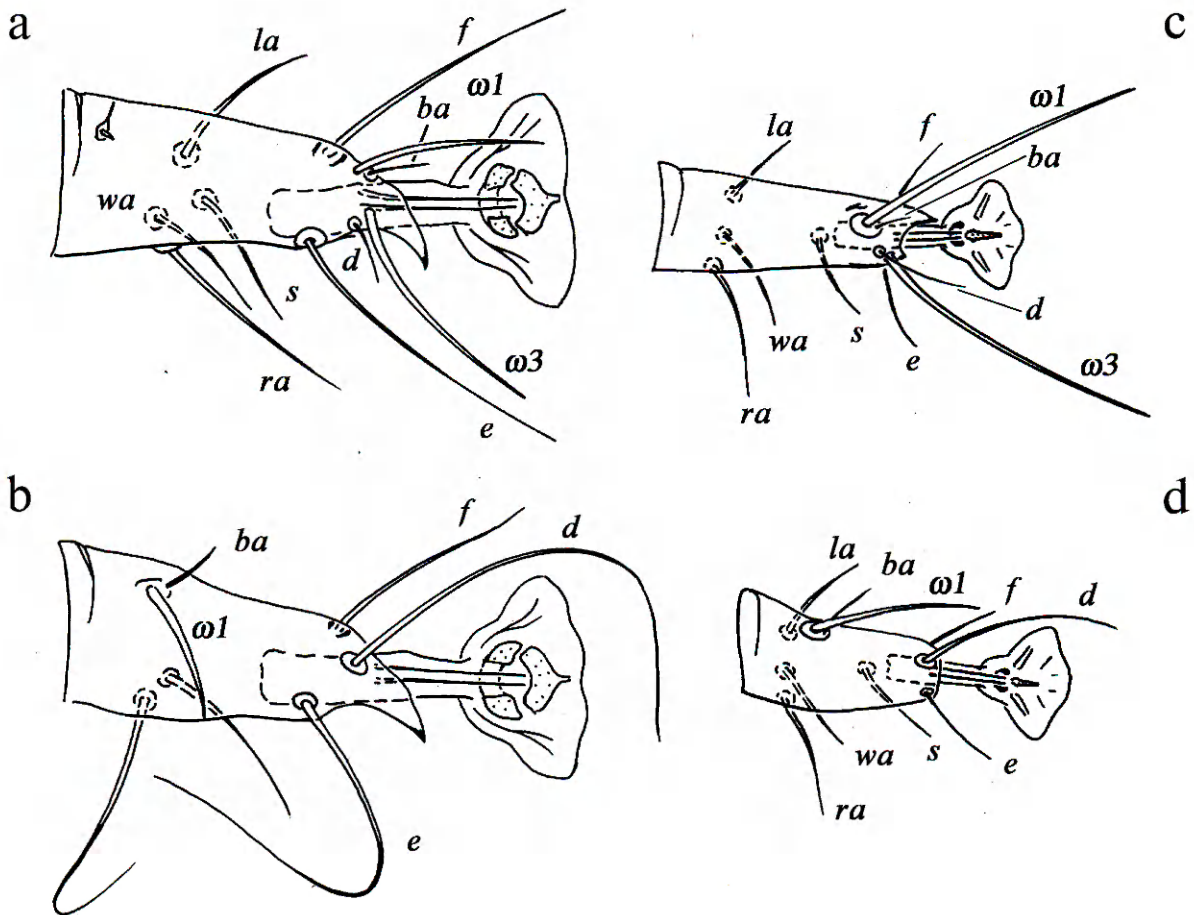


Fig. 3. Tarsi I, II of mites of the superfamilies Psoroptoidea and Pyroglyphoidea. a — *Otodectes cynotis* (Hering) (Psoroptoidea, Psoroptidae), right tarsus I of female, b — same, right tarsus II, c — *Dermatophagoides pteronyssinus* (Trouessart) (Pyroglyphoidea, Pyroglyphidae), right tarsus I of female, d — same, right tarsus II.

plumage and skin of birds. The superfamily Pyroglyphoidea is apparently the youngest lineage of feather mites within Psoroptida. As for relationships of Pyroglyphoidea to other superfamilies of Psoroptida, this group shares common features with Analgoidea (sensu O'Connor) and Psoroptoidea (permanent parasites of mammals) by having a condylophore guide and lacking proral and unguinal setae on all tarsi. The superfamily Pyroglyphoidea is also characterized by the apical position of the solenidion $\omega 1$ on tarsus I (Fig. 3 c, d). This characteristic is a common feature among most taxa of Psoroptoidea (Fig. 3 a, b) that indicates close phylogenetic relationships of these superfamilies. In many families of Psoroptoidea, the representatives of which have the apical position of solenidion $\omega 1$ on tarsi I, this solenidion on tarsi II may also occupy an apical position [Fain, 1963]. Nevertheless, a convergence origin of such characteristics as an apical position of solenidion $\omega 1$ in Pyroglyphoidea and Psoroptoidea may not be excluded. Gaud and Atyeo [1996] decided that such

characteristics as an apical position of the solenidion $\omega 1$ on the anterior tarsi in Pyroglyphidae and Ptyssalgidae could be a convergence with Psoroptoidea, and placed these families into Analgoidea.

The creators of both general taxonomic systems of feather mites did not pay much attention to phylogenetic relationships between the major taxa of feather mites. Originally, the three superfamilies [sensu Gaud and Atyeo, 1978] simply referred, without comments, to a monophyletic line, a sister line to Psoroptoidea [Krantz, 1978]. Further, all experts have come to agree that feather mites represent at least a diphyletic grouping with Analgoidea, derived from one psoroptidian phylogenetic line, and Pterolichoidea plus Freyanoidea from another [Aty eo, Gaud, 1979a, Gaud, Atyeo, 1982a, 1996; OConnor, 1982a, 1982b, 1984, 1994; Dabert, Mironov, 1999; Mironov, 1999; Proctor, 2003]. In regard to Pterolichoidea and Freyanoidea, their relationships do not make here any problem. Either they are sister lineages, or Freyanoidea derived from the core of Pterolichoidea, in any case these

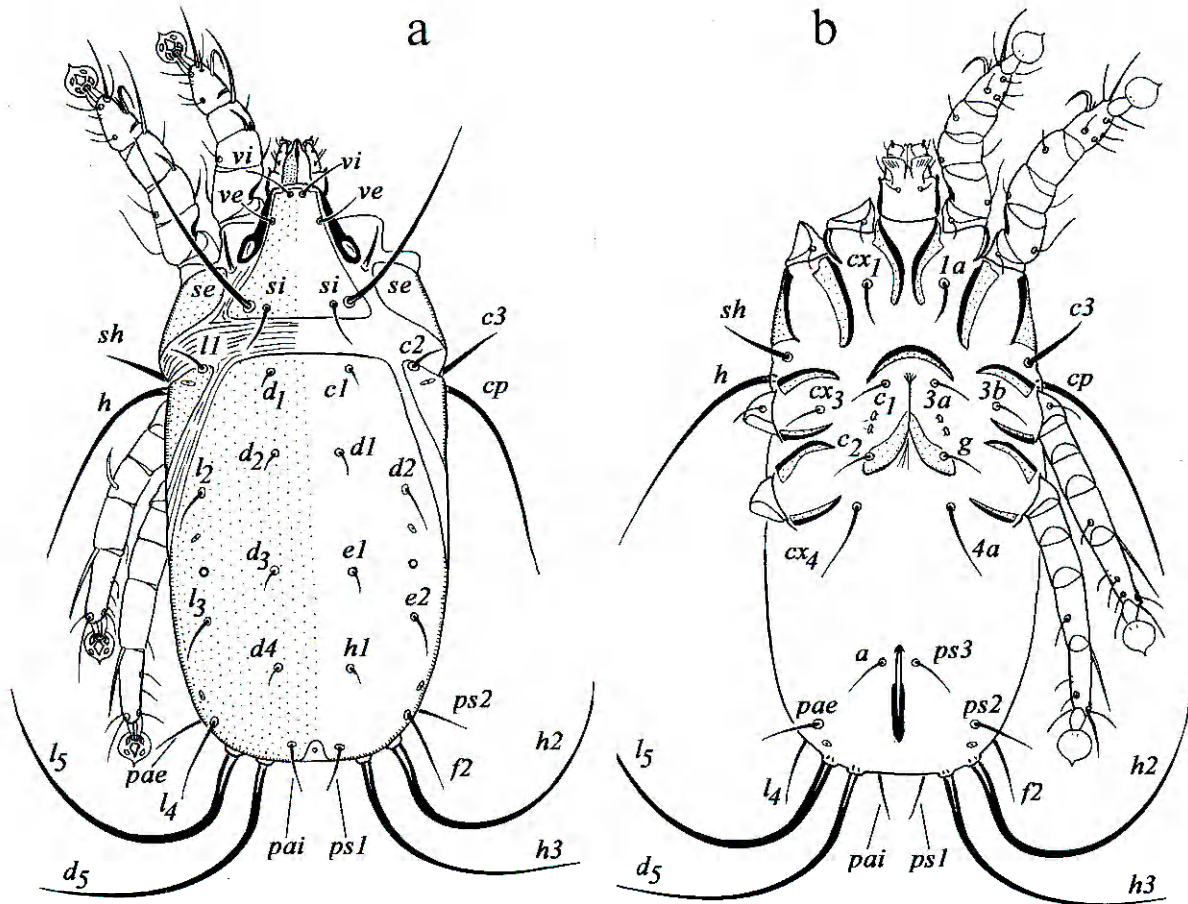


Fig. 4. Assignment of two nomenclature systems for idiosomal chaetotaxy of feather mites.

a — dorsal view, b — ventral view. Designations on the left side of the schematic drawing of female — Atyeo and Gaud [1966, 1971], designations on the right side — Griffiths et al. [1990].

taxa form a single major lineage. As for the Analgoidea lineage, it is obviously closer to Psoroptoidea than to Pterolichoidea lineage [Aty eo, Gaud, 1979a; O'Connor, 1982a; Dabert, Mironov, 1999]. If we consider the lineage of Pyroglyphoidea to be a separate lineage deserving the taxonomic rank of superfamily, we have to conclude that feather mites are triphyletic, i.e. psoroptidian mites (Psoroptidia) had conquered birds as a host group three times independently. This conclusion even does not depend upon whether Pyroglyphoidea is actually closer to Analgoidea or Psoroptoidea. In any case, the presence of free-living forms in Pyroglyphoidea obviously seems to be an ancestral feature and their rare and mosaic distribution only on higher orders of birds (higher terrestrial Neognathae), mainly Passeroformes, Piciformes, and Psittaciformes, [Gaud, 1968; Fain et al., 1988; Fain, Atyeo, 1990], indicates that it is the youngest lineage of feather mites among Psoroptidia. The two other major lineages, Analgoidea and Pterolichoidea (*sensu lato*), are associated with all recent orders of birds, beginning from the Ratites, and on all bird orders

they are represented by extremely specialized groupings, highly restricted in their distribution among hosts taxa and often demonstrating a pattern of coevolution with a respective host group [Peterson, 1975; Gaud, Atyeo, 1979, 1980, 1982a, 1996; Dabert, Mironov, 1999; Mironov, Dabert, 1999, Ehrnsberger et al., 2001].

Thus, two different concepts concerning the macrosystem of feather mites exist. What system is better and should be followed? The system presented by Gaud and Atyeo is a taxonomic basis for the excellent modern manual "Feather mites of the World" [Gaud, Atyeo, 1996], which may be referred to as the "Bible of feather mites". Naturally, it is and will be in successful practical use among numerous investigators for systematics and biodiversity of feather mites for a very long time. However, it incorporates only astigmatid mites, which are "feather mites" by their mode of life, and leaves out of the frame of study several derived lineages, the representatives of which have developed another forms of parasitism on birds. At the same time, O'Connor's system

[1982a] is not so detailed and concerns only higher taxa, but apparently more adequately reflects phylogenetic relationships among feather mite superfamilies and other the major astigmatid taxa. Taking in attention an interest to astigmatid mites noticeably growing in present time among acarologist, it wants to believe that future taxonomic phylogenetic investigations based on different methods, including morphological and molecular ones, would help to recover phylogenetic relationships among most groups of feather mites both on higher and species levels.

In conclusion, it would be expedient to propose a practical and rather conventional determination for the mite group in question: feather mites are a paraphyletic ecological group of psoroptidian mites, characterized by permanent parasitism on the plumage or skin of birds, and represented according to current taxonomic concepts by several taxa of superfamilial rank. Since the term "parasites" is may or may not be accurate, it may be avoided in this definition and substituted by another term, such as "symbiotes" or "commensals." Whether the term "parasites" is appropriate in this instance depends on which of the definitions of "parasitism" the investigator follows. However, the questions of whether feather mites are true parasites or not, and what groups of feather mites may be considered parasites, pertain to the field of general biology.

2. Homology of setae in idiosomal chaetome

The second important problem in the study of feather mite concerns the homology of some idiosomal setae, and, respectively, the assignation of chaetotactic nomenclature to them. As experts who deal with Astigmata very well know, two basic nomenclatural systems for idiosomal chaetotaxy currently exist (Fig. 4). One of these systems was originally created by Zachvatkin [1937, 1941, 1953] mainly for use with free-living astigmatids. Today, a version of this system proposed by Atyeo and Gaud [1966, 1971] is most widely used when dealing with parasitic astigmatid mites. The second system derives from the one elaborated by Grandjean [1933, 1934a, 1934b, 1939] for use with oribatid mites (Oribatei). Griffiths et al [1990] adapted the latter system so it could be used for astigmatid mites, and compared the two basic nomenclature systems, as interpreted by various recent authors. I would not discuss here any advantages and disadvantages of these nomenclature systems, because both of them can be used in

practice, and the standard and most widely used versions of these systems for any of the groups of Astigmata [Atyeo, Gaud, 1966; Griffiths et al., 1990] are easily convertible (Fig. 4).

The problem of the homology of ventral hysterosomal setae in feather mites, and also in other groups of parasitic Astigmata, where the position of ventral setae is significantly distorted in comparison to free-living forms, concerns only the coxisternal setae situated in the areas of coxae III, IV and genital setae. This problem consists of two main questions: a) the homology of these setae between males and females in the same taxon; b) the homology of these setae between primitive forms (including free-living taxa of astigmatans), and derived forms with a significantly modified position of setae. Griffiths and coauthors [Griffiths et al., 1990] only briefly mentioned that among feather mites "some signature assignments are uncertain at best", and indicated the family Gabiciniidae as an example. However, this problem actually remains unsolved for a number of feather mite taxa. Discordance may be noticed, if one compares the manner in which nomenclature is assigned to some related taxa in papers of different experts, or even in different papers of a single given expert.

The areas of coxae III, IV (coxal fields) and genital area of ventral hysterosoma carry only 4 pairs of setae. Comparative assignation of two basic nomenclature systems for the case of the most common and apparently archaic positions of setae in analgoid feather mite, with an example of female, is given in Fig. 4. It corresponds to the assignation widely used for many groups of free-living Astigmata (Fig. 5 c, d). A single pair of setae always occupies the centers of coxal fields III, and only they are, indisputably, the setae of coxae III. These setae are referred to as setae *cxIII* by Atyeo and Gaud [1966], and as setae *3b* by Griffiths et al. [1990]. Three other setal pairs, both in males and females, are situated in the median part of the hysterosoma, and often arranged in some kind of two longitudinal rows (setae *3a, g, 4a* of Griffiths et al. [1990], or *c1, c2, cxIV* of Atyeo and Gaud [1971]. In earlier versions of Zachvatkin's system used by Atyeo and Gaud [1966] these setae are respectively referred to as *c1, c2, c3*, and in the version modified by Fain [1963, 1967] — *ga, gm, gp*.

The discussion below concerns namely these three pair of setae, therefore for the sake of simplicity I refer only to them as "ventral hysterosomal setae". As these pairs in most cases are disposed

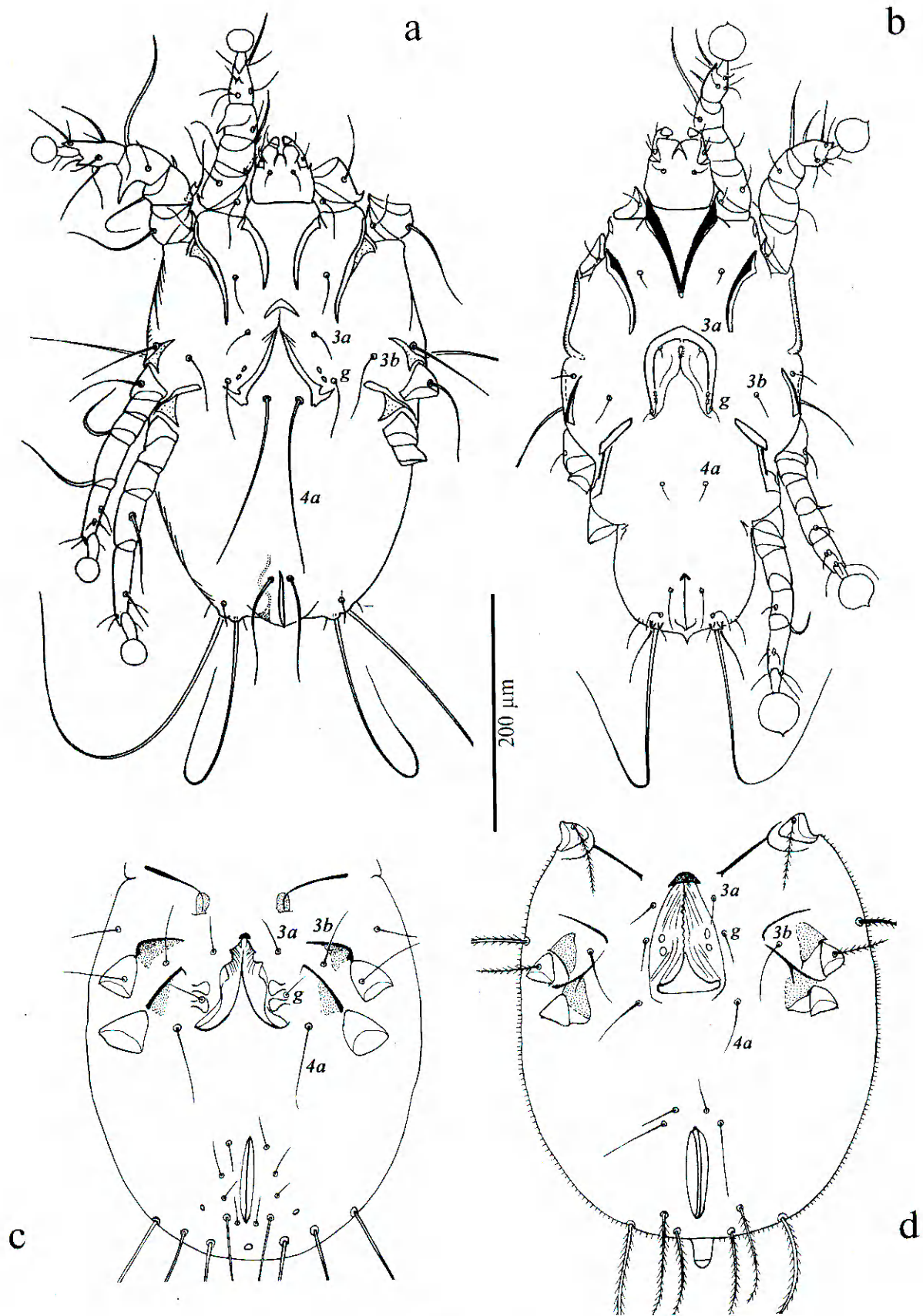


Fig. 5. Assignment of setal nomenclature for ventral hysterosomal setae in females of Analgoidea and free-living Astigmata. a — *Megninia californica* Mironov et Galloway (Analgidae) (Hypothesis 1), b — *Bdellorhynchus polymorphus* Trouessart (Avenzoariidae) (Hypothesis 1), c — *Tyrophagus putrescentiae* (Schrank) (Acaridae), d — *Glycyphagus domesticus* (De Geer) (Glycyphagidae). Modified drawings after: a — Mironov, Galloway [2001a], c, d — Fain et al. [1988].

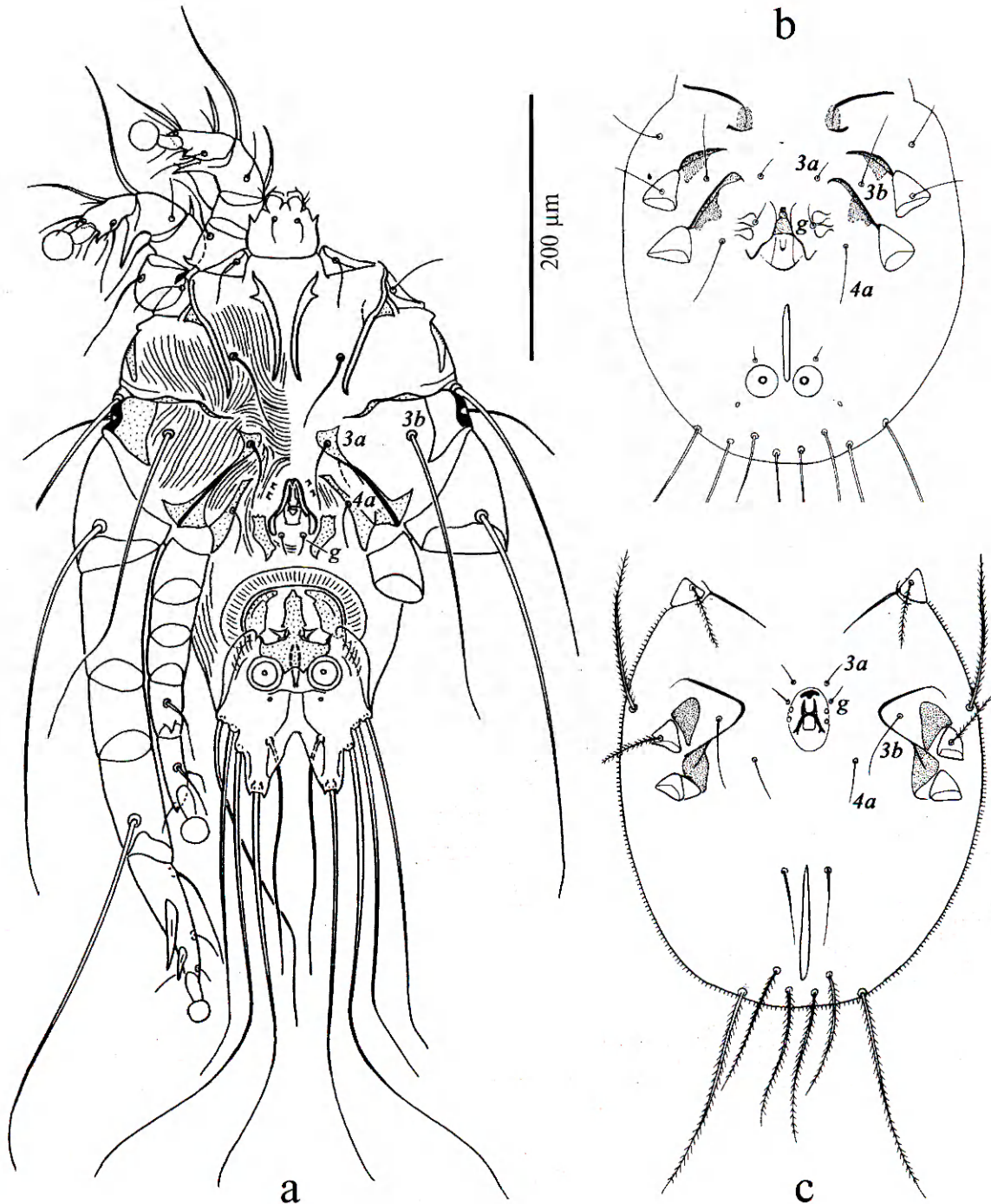


Fig. 6. Assignment of setal nomenclature for ventral hysterosomal setae in males of Analgoidea and free-living Astigmata. a — *Megninia californica* Mironov et Galloway (Analgoidea) (Hypothesis 1), b — *Tyrophagus putrescentiae* (Schrank) (Acaridae), c — *Glycyphagus domesticus* (De Geer) (Glycyphagidae). Modified drawings after: a — Mironov, Galloway [2001a], c, d — Fain et al. [1988].

one after another along the median line of the mite body, to indicate their topographical position, in the discussion given below I refer primarily to them as the first, second and third pair, respectively, and then propose signature assignments according to possible hypotheses. The nomenclature system used in the discussion is that of Griffiths et al. [1990].

It seems most expedient to begin considering the homology of these setae in the superfamily Analgoidea, because in most its families their arrangement is quite similar, and it is also easy to compare this arrangement to those in free-living forms of Astigmata, such as Acaridae and Glycyphagidae, and to trace the homology of setae (Figs.

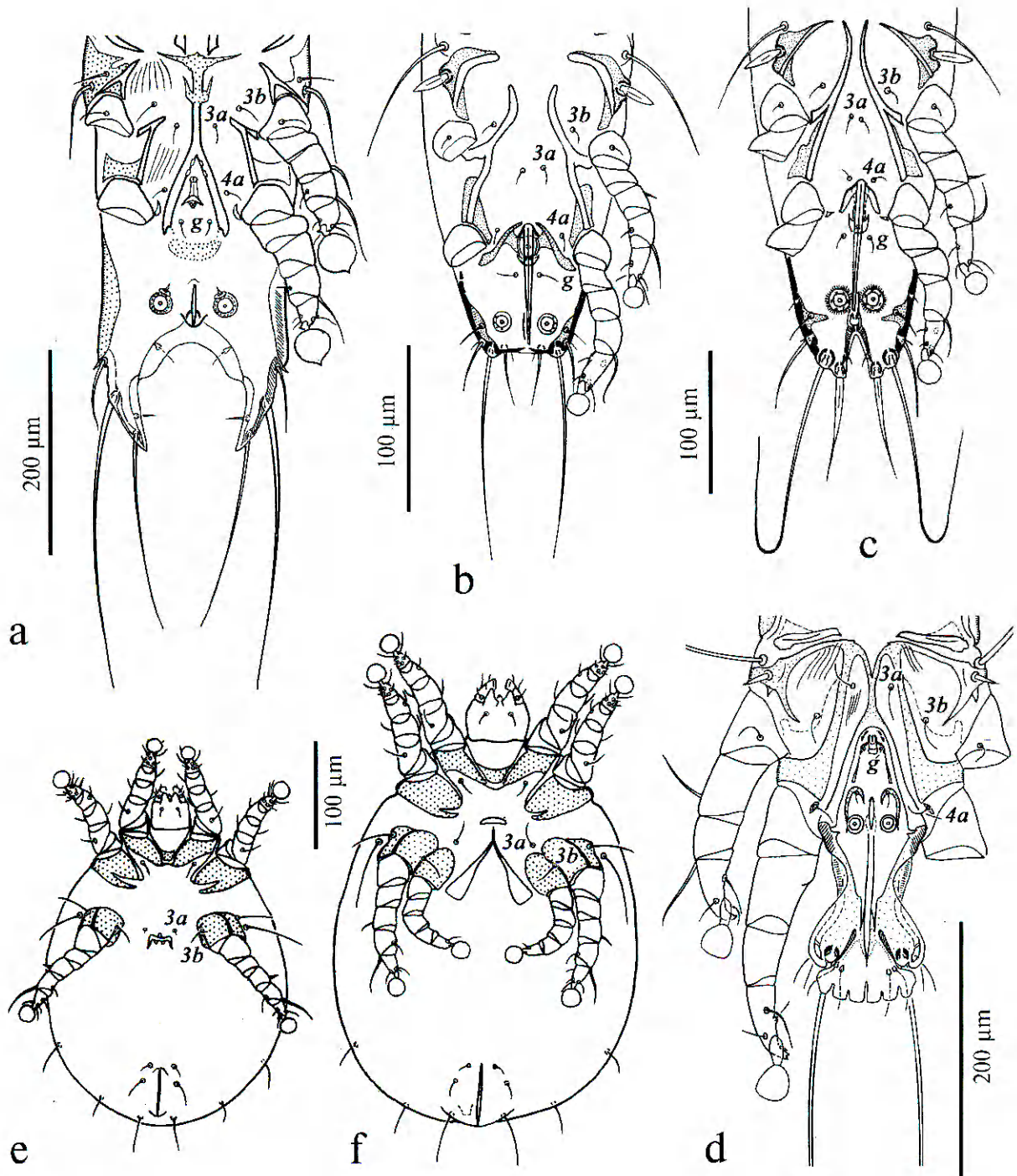


Fig. 7. Assignment of setal nomenclature for ventral hysterosomal setae in Analgoidea according to hypothesis 1. a — *Bregetovia selenura* (Megnin et Trouessart) (Avenzoariidae), b — *Pedanodectes marginatus* Mironov et Kopij (Proctophyllodidae), male, c — *Montesauria emberizae* Mironov et Kopij (Proctophyllodidae), male, d — *Megaloptes triphyllurus* Mironov et Perez (Alloptidae), male, e — *Atelespoda minuta* Vasyukova et Mironov (Apionacaridae), male, f — same, female. Modified drawings after: b, c — Mironov, Kopij [1997], d — Mironov, Perez [2000], e, f — Vasyukova, Mironov [1991].

5 c, d, 6 b, c). According to the concept of Griffiths et al. [1990], the first setae belongs to coxae III, the third — to coxae IV, i.e. they belong to the metapodosoma, while only the second pair represents the genital setae and belongs to the next body tagma, opisthosoma. In females of Analgoidea, the first pair is usually situated at the transverse level of the

anterior end of the egg opening (or slightly posterior to the epigynum if it is present), the second pair is at the level of the posterior angles of the egg openings, and the third pair is at the level of trochanters IV or posterior to them (Figs. 4, 5 a, b). Here it is important to note, that the setae of the third pair in Analgoidea are closer to each other,

than those of the other two pairs. In females of all taxa of Analgoidea, the anterior pair is usually referred to as *3a*, the second pair — *g*, the third pair — *4a* [Griffiths et al., 1990]. According to Atyeo and Gaud [1966, 1971], the first and second setae are genital setae (*c1* and *c2* in their nomenclature system), while the third pair only belongs to the coxae IV and is referred as to setae *cxIV*. In females of free-living Astigmata, the members of the third pair (*4a*) are most distant from each other, while the members of the second pair (*g*) are significantly close to each other than the setae *4a* (Figs. 5 a, b). Thus, both nomenclature systems suggest that in analgoid mites, the egg opening belonging to opisthosoma has moved forward, topographically to the level of metapodosoma, while coxal areas IV belonging to metapodosoma, have moved toward each other and probably joined together at midline of the body (Figs. 4, 5 a, b).

In males of most analgoid taxa (with the exception Proctophyllodidae, and Apionacaridae, which are considered separately below), the first pair is situated approximately at the level of the coxal setae *3b*; if the coxal fields III are heavily sclerotized, these setae are commonly disposed in their inner margins or on tips of epimerites IV. The second pair of setae in question is situated at the level of the genital apparatus, and these two setae are usually very widely separated; in most taxa, it is rather obvious that they occupy the areas of coxae IV (Fig. 6 a). Only in some representatives of Alloptidae, the setae of the second pair are significantly moved posterior and topographically appear as “the third pair”, but they are situated in the most lateral angles of the coxal fields IV and their belonging to coxae IV is obvious (Fig. 7 d). This is the reason why, in analgoid males, these setae are indisputably considered to be the coxal setae *4a*. The third pair of ventral hysterosomal setae, the members of which are the closest to each other, is situated at the base of the genital arch (Figs. 5 a, 7 a–c). The close relationship of these setae with the genital apparatus obviously suggests that, in a functional sense, they are the genital setae. In such free-living astigmatid mites as Acaridae and Glycyphagidae, the second pair (*g*) is usually situated at the midlevel of the genital apparatus or at the level of its apex; and these setae are always rather distant from each other, usually as the setae *3a* (Fig. 6 b, c). The members of the third pairs (*4a*) in free-living Astigmata are widely separated from each other, and it seems indisputable that they belong to the areas of coxae IV. The homology of setae in

males and females of Analgoidea described above may be referred as hypothesis 1 (Figs. 5 a, b; 6 a).

The position of the three hysterosomal setae in question in males of Proctophyllodidae is not in a contradiction to hypothesis 1. Examination of various forms of Proctophyllodidae makes it easy to imagine how, due to a significant elongation and narrowing of the idiosoma, the members of the second pair have moved to the midline, and in the result of this modification all the three pairs of ventral hysterosomal setae often form two almost straight longitudinal rows (Fig. 7 b, c).

The disposition of setae in Apionacaridae also supports hypothesis 1. In both sexes of this family, only one of the three pairs in question remains, while the other two are lost. In females, the remaining pair is situated at the level of anterior end of the egg opening, and in males, this pair is anterior to the genital apparatus and situated approximately at the level of coxal fields III. It is reasonable to conclude that the remaining pair both in males and females is the coxal setae *3a* (Fig. 7 e, f).

Only one aspect of the genus *Diplaegidia* Hull, 1934 (Analgoidea, Megniniinae) raises certain doubt in this hypothesis. Normally, in both sexes of this genus, one of the three ventral hysterosomal pairs of setae in question is duplicated. From the first glance, it seems reasonable and logical to suggest that the same complex of genes should control the duplication both in males and females. However, if this suggestion was assumed to be true, then hypothesis 1 would turn out to be incorrect. In *Diplaegidia* males, the setae referred to as the genital setae *g* are duplicated (Fig. 8 b), while in females, the duplicated pair of setae is the coxal setae *4a* (Fig. 8 a). Thus, if we think strongly to follow hypothesis 1, we have to admit that such an extremely rare event among astigmatid mites as a duplication of setae may take place in one species in non-homologous pairs of ventral setae. If we suggest that the duplication of setae in astigmatids could take place only in homologous setae (as an indisputable rule), we have to conclude that the duplicated setae are either the genital setae *g*, or the coxal setae *4a*. In my opinion, if this rule is assumed to be true, it would be most reasonable to suggest that the third pair in Analgoidea females is the genital setae *g*, which did not move anterior, along with the genital opening, while two anterior pairs flanking the egg opening are the coxal setae *3a* and *4a* (Fig. 8 c). This extravagant concept may be referred to as hypothesis 2. Additional arguments and suggestions supporting this hypothesis are as

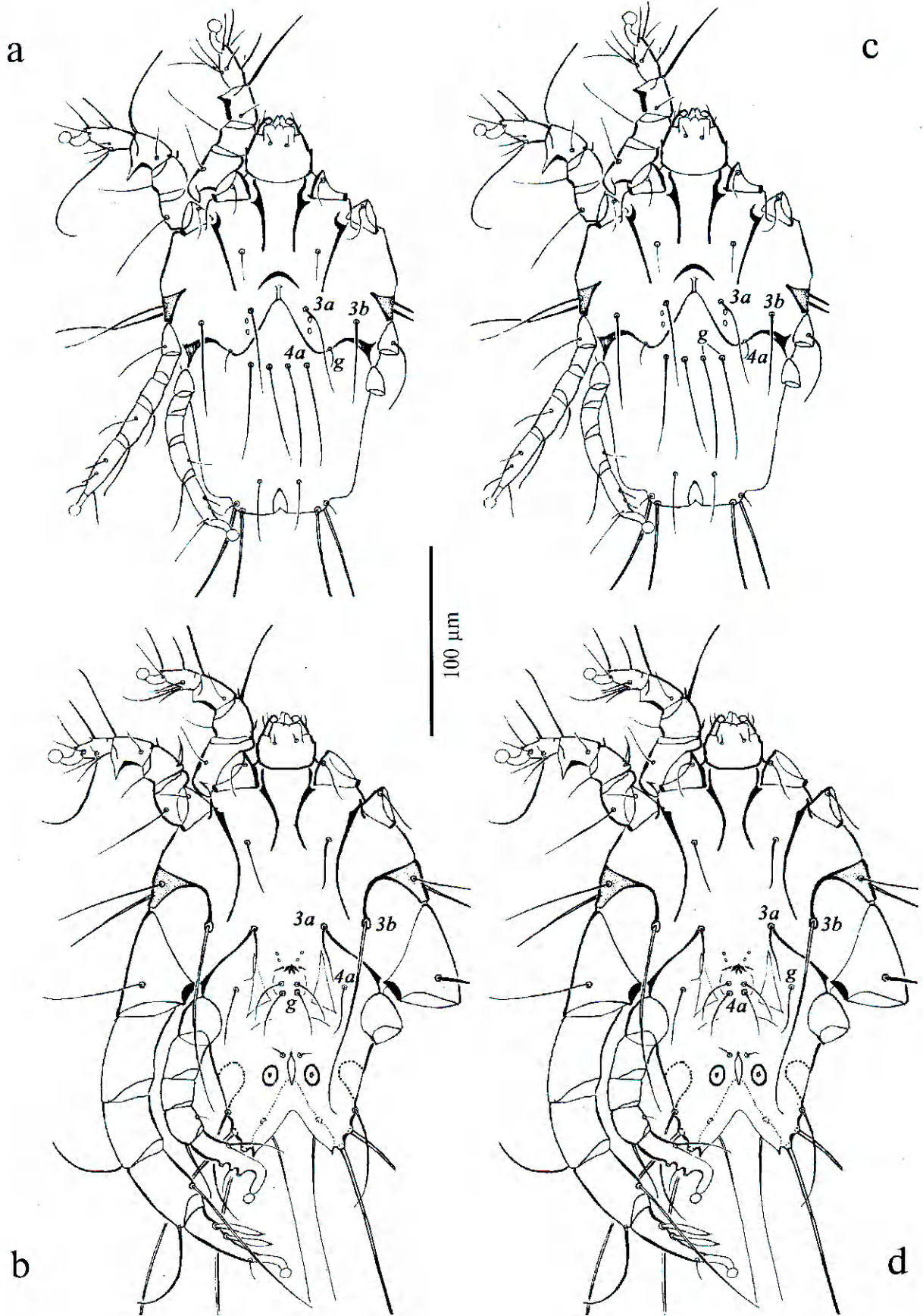


Fig. 8. Assignment of setal nomenclature for ventral hysterosomal setae in males and females of *Diplaegidia femorata* Gaud according to hypotheses 1 and 2. a — female, hypothesis 1, b — male, hypothesis 1, c — female, hypothesis 2, d — male, unbelievable hypothesis.
a-d — after Gaud [1976], modified.

follows: in analgoid males, the second pair in obviously belongs to the coxal fields IV; in females, members of the third pair are very close to each other (as is the third pair in males); in both sexes, the setae, which are situated posterior to the genital apparatus and adjacent to each other, most probably belong to the genital segments of the opisthosoma, rather than to setae, which are widely spread apart and moved forward to the body's sejugal region.

Sure, it is possible to suggest that in males, the second of setae situated on coxal fields IV is the genital setae *g*, while the third (duplicated pair) situated at the base of the genital apparatus is setae of coxae IV (*4a*). In the case of this suggestion, it appears that the homologous pairs are duplicated in males and females of *Diplaegidia* (compare Figs. 8a and 8d), but mutual exchange of normal positions of the coxal IV (*4a*) and genital (*g*) setae in males seems quite unbelievable.

Thus, in regard to the unique case of setal duplication in *Diplaegidia*, it is most reasonable to conclude that non-homologous pairs are duplicated in males in females of this genus and follow hypothesis 1 of nomenclature assignment (Figs. 8 a, b).

Analysis of homology of the ventral hysterosomal setae in Pterolichoidea and Freyanoidea is more complicated, especially in regard to males, because some cases of setae arrangement provide the basis for several controversial hypotheses. However, first of all, it is necessary to point out that the positions of ventral hysterosomal setae in females of these superfamilies are quite similar to those of Analgoidea and other supafamilial taxa of Astigmata, and it is easily to recognize the homology of setae, and hypothesis 1 may be easily applied (Figs. 5 a–d, 9 a–d). It is important to notice that, for unclear reasons, the nomenclature assigned to the two anterior pairs of setae (setae *g* and *3a*) in some drawings of pterolichoid females is opposite of that used for analgoids [for example see Gaud and Atyeo, 1996: Figs. 8, 343, 365, 395, 405]. These authors probably assigned names to the setae based on their position in relation to the genital acetabulae and referred the first pair of setae in question as the genital setae *g*. However, it is not a strong argument, because the position of setae relative to the acetabulae is quite variable in feather mites, and often it is not similar even in males and females of the same species. Considering Pterolichoidea and Freyanoidea, it is necessary to discuss separately each grouping of families characterized by specific arrangements of the ventral hysterosomal setae.

In males of the families Freyanidae and Vexillariidae (Freyanoidea), the position of the three pairs of the ventral hysterosomal setae resembles that in Analgoidea (Figs. 5 a, b, 10 a–c). It is worthy to point out that the third pair of setae is situated distinctly posterior to the base of the genital apparatus and the second pair is always anterior to the apex of the genital apparatus, while the position of the latter setae is significantly variable in their distance from the midline among the genera. In most derived taxa of Freyanidae, the close association of the third pair with the genital apparatus is visible more clearly, while the members of the second pair are often found in the sclerotized coxal fields IV. The location of these setae is good evidence that the second pair is the coxal setae *4a*, and the third pair of setae is the genital setae *g* (Fig. 10 a–c). In cases where they are actually closer to each other than members of the third pair (Fig. 10 d), it is possible to suggest that they have simply moved from the centers of the coxal fields to the midline. According to these arguments, the third pair is the genital setae *g*. Therefore, the disposition of the ventral hysterosomal setae looks homologous to that in Analgoidea (Fig. 6 a), and the chetotaxy nomenclature may be reasonably applied according to hypothesis 1 (Fig. 10 a–d, right designations). Vasyukova and Mironov [1991] used this alternative for Freyanidae.

According to another concept, the second pair in males of Freyanoidea may be considered as the genital setae *g*. In some taxa (Freyanidae: Burhincarinae), these setae are situated anterior and slightly lateral to the genital apparatus (Fig. 10 d), in contrast to their location in Analgoidea. In this case, the third pair is the coxal setae *4a*, which have obliquely moved from the centers of coxal field IV to the midline and posterior to the genital apparatus. This disposition of the ventral hysterosomal setae resembles quite well their disposition in free-living Astigmata (Fig. 6 b, c). This concept in regard to males of Freyanoidea and also to ones of Pterolichoidea (see below) may be referred to as hypothesis 3 (Figs. 10 a–d, left designations). The most serious counterargument to this notion in regard to Freyanoidea is the fact that the second pair distinctly occupies coxal fields IV in most taxa of this superfamily (Fig. 10 a, b). Dabert [1987], Mironov and Dabert [2001] assigned the chetotaxy nomenclature to Freyanidae according to this hypothesis. The following argument suggests that hypothesis 1 is more logical than hypothesis 3. It is more reasonable to suggest that the setae, which are

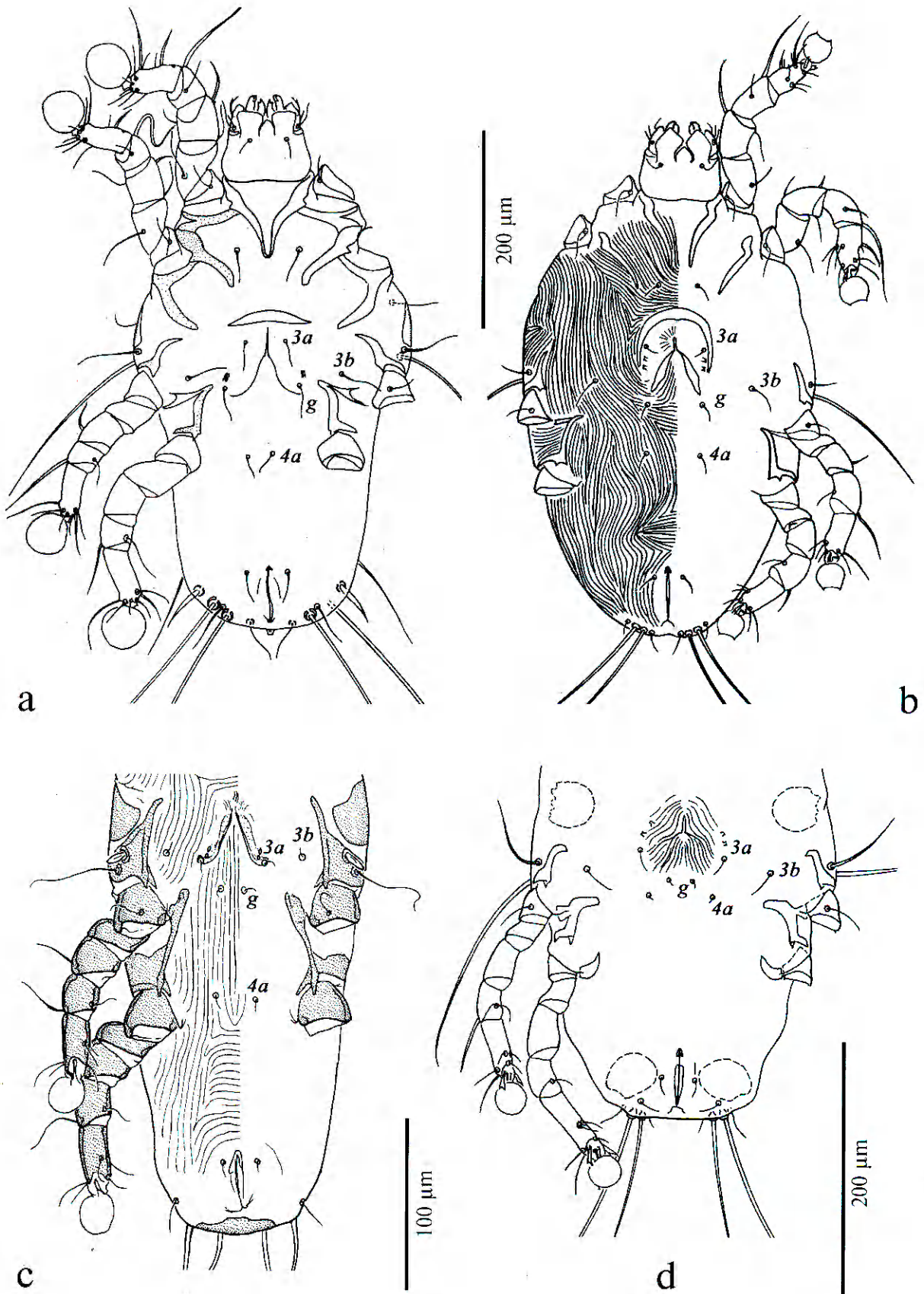


Fig. 9. Assignment of setal nomenclature for ventral hysterosomal setae in females of Freyanoidea and Pterolichoidea according to hypothesis 1. a — *Cernyella howei* Mironov et al. (Freyanidae, Burhinacarinae), b — *Pseudolichus phasiani* Mironov (Pterolichidae), c — *Montchadskiana tyrrelli* (Trouessart) (Pterolichidae, Magimeliinae), d — *Nymphicilichus perezae* Mironov et Galloway (Pterolichidae, Pterolichinae, *Psittophagus* generic group). Modified drawings after: a — Mironov et al. [2001], b — Mironov [1997], c — Dabert, Ehrnsberger [1999], d — Mironov, Galloway [2002b].

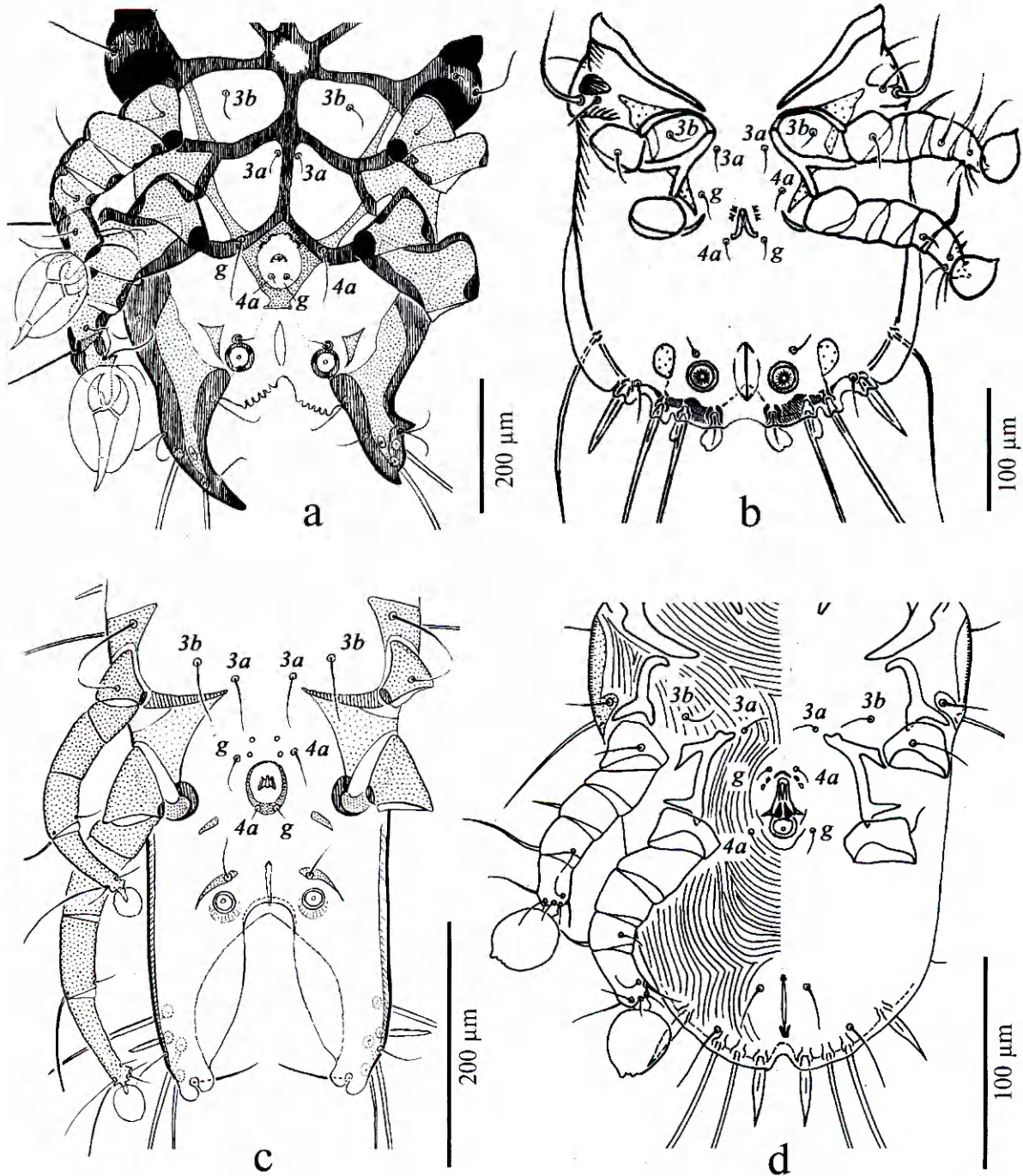


Fig. 10. Assignment of setal nomenclature for ventral hysterosomal setae in males of Freyanoidea according to hypotheses 1 and 3. a — *Sulanyssus caputmedusae* Trouessart (Freyanidae, Michaeliinae), b — *Freyana dubinini* Vasyukova et Mironov ((Freyanidae, Freyaninae), c — *Calaobia circinigera* (Megnin et Trouessart) (Vexillariidae, Calaobiinae), d — *Monofreyana collaris* Mironov et Dabert (Freyanidae, Burhinacarinae). Designations on the right side — hypothesis 1, designations on the left side — hypothesis 3.

Modified drawings after: a — Gaud, Atyeo [1982b], b — Vasyukova, Mironov [1991], c — Gaud, Atyeo [1990], d — Mironov, Dabert [2001].

found closer to the genital apparatus are really genital setae in origin, i.e. they belong to the opisthosomal tagma, than to suggest that true genital setae have moved onto the areas of coxal fields IV, and at the same time true coxal setae IV have moved back and to the median line, topographical-

ly from metapodosoma to opisthosoma, to substitute functionally the true genital setae.

The positions of the ventral hysterosomal setae in males of the superfamily Pterolichoidea setae significantly vary among families; this fact provides material for controversial hypotheses. Be-

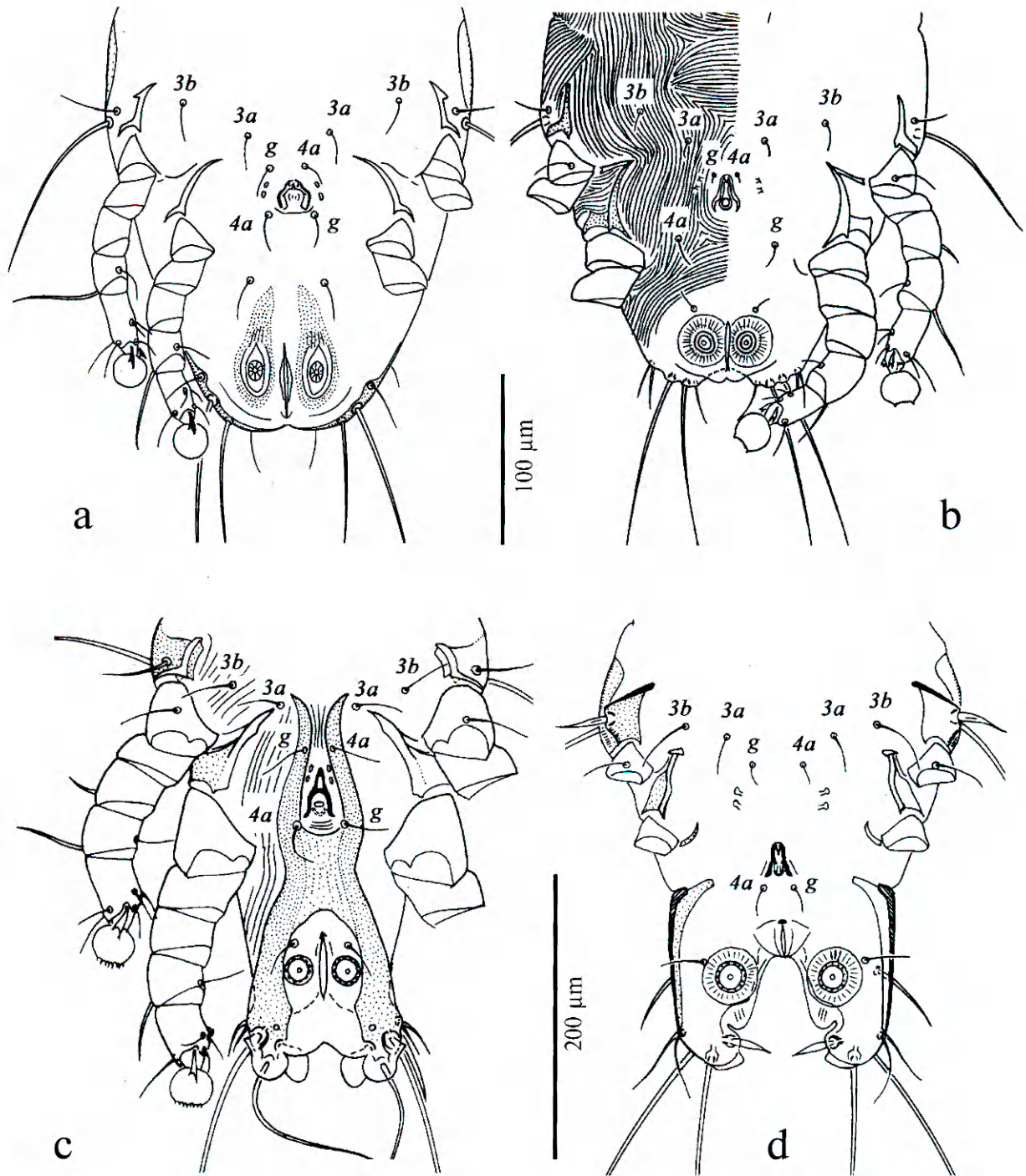


Fig. 11. Assignment of setal nomenclature for ventral hysterosomal setae in males of Pterolichoidea according to hypotheses 1 and 3. a — *Corydolichus calandrellicolus* Mironov et Sayakova (Ochrolichidae), b — *Pseudolichus phasiani* Mironov (Pterolichidae, Pterolichinae), c — *Apexolichus lathami* Mironov et al. (Pterolichidae, Pterolichinae, *Protolichus* generic group), d — *Aetacarus* sp. (Gabuciniidae). Designations on the right side — hypothesis 1, designations on the left side — hypothesis 3. Modified drawings after: a — Mironov, Sayakova [2001], b — Mironov [1997], c — Mironov et al. [2003].

sides, the family Pterolichidae, which is the largest and forms a core of the superfamily, is apparently paraphyletic [Ehrnsberger et al., 2001] and its representatives demonstrate rather different arrangements of the ventral hysterosomal setae. Therefore, some pterolichid taxa below the familial rank are consid-

ered here as separate subdivisions equal in taxonomic sense to families. In regard to the disposition of the ventral hysterosomal setae, most families of Pterolichoidea may be arranged into two groups.

The first group includes the families Ascouracaridae, Cheylabididae, Kiwilichidae, Ochroli-

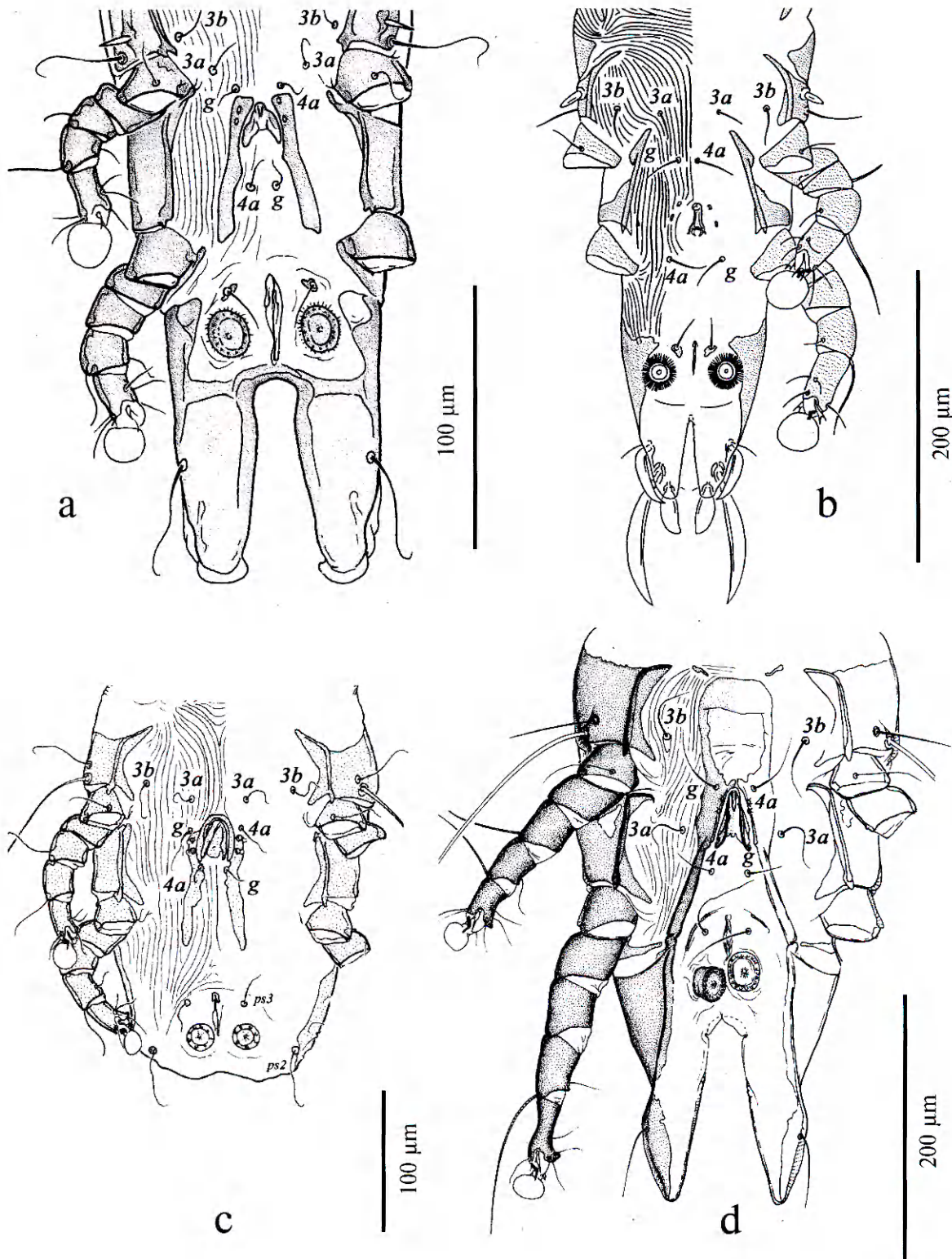


Fig. 12. Assignment of setal nomenclature for ventral hysterosomal setae in males of Pterolichoidea according to hypotheses 1 and 3. a — *Sokoloviana vanelli* Dabert et Ehrnsberger (Ptiloxenidae), b — *Triphyllochaeta charadrii* Dubinin (Pterolichidae, Magimeliinae), c — *Grenieria simplex* (Trouessart) (Syringobiidae), d — *Limosilichus limosae* Vasyukova et Mironov (Syringobiidae). Designations on the right side — hypothesis 1, designations on the left side — hypothesis 3. Modified drawings after: a — Dabert, Ehrnsberger [1996], b — Mironov et al. [2002], c — Dabert, Atyeo [1997], d — Dabert [2003].

chidae, Oconnoriidae, Rectijanuidae, and the subfamilies Pterolichinae and Xoloptoidinae (Pterolichidae). In males of these mites, the second pair of

ventral hysterosomal setae is situated slightly anterior (or, rarely, lateral) to the genital apparatus, and these setae are very close to each other. In

contrast, the third pair is quite distant from the genital apparatus, the setae are distant from each other, and it is rather clearly visible that they occupy the area of coxal fields IV (Fig. 11 a–c). This disposition is decidedly similar to that free-living Astigmata, such as Acaridae and Glycyphagidae (Fig. 5c, d). Therefore, the assignation of the chaetotaxy nomenclature according to the hypothesis 3 seems to be absolutely justified (Fig. 11 a–c, left designations).

The second major group of pterolichoid taxa includes the families Falculiferidae, Gabuciniidae, Karmereillidae (except the genus *Pseudogabucinia* Cerny, 1961), subfamilies Ardeacarinae, Ardealaginae, generic group *Protolichus*, and the genera *Gymnolichus* Gaud et Mouchet, 1961, *Struthiopteroichus* Dubinin, 1955 (Pterolichidae: Pterolichinae). In males of this group, the second pair of the ventral hysterosomal setae is anterior to genital apparatus and quite distant from it (Fig. 11 c, d). The third pair is posterior to the genital apparatus, situated near its base, and these setae are close to each other. An additional piece of evidence to support the argument that the third pair is the genital pair (g) is the presence of genital apodemes in the *Protolichus* generic group (Pterolichidae: Pterolichinae) (Fig. 11 c). It does not matter whether the apodemes are derivatives of the inner margin of coxae IV (i.e. part of metapodosoma) of newly formed structures of opisthosoma; in all cases, the third pair of setae is between the apodemes. The position of the third pair in the second group of pterolichoids is quite similar to that in Analgoidea (Fig. 6a). As it was suggested for Proctophyllodidae (Analgoidea), it is possible that the members of the second pair, which are coxal setae in origin, have simply moved to the midline and slightly forward, and the setae of the third pair have moved from the anterolateral position to the genital apparatus and to the posterior position. Therefore in accordance with this concept, hypothesis 1 can be rather reasonably applied to the said groups of pterolichoid mites (Figs. 11 c, d, right designations). Granted, the resemblance to Analgoidea might only be a superficial one, and the second pair may be the genital pair (g), which has moved far anterior from the genital apparatus, while at the same time the coxal setae IV (4a) may have “traveled” far posterior and to the median line, topographically onto opisthosoma, and reached a position posterior to the genital apparatus. If this scenario is true, it means that the coxal fields IV have joined together and crossed the opisthosoma,

because these setae obviously moved together with respect to the surfaces of the coxae. Only if these modifications are admitted, the chaetotaxy nomenclature may be applied according to hypothesis 3.

In regard to the families Ptiloxenidae and Syringobiidae, and the subfamily Magimeliinae (Pterolichidae), it is possible to say that these taxa are intermedial between the two groups of pterolichoids considered above, because in males of these taxa, members of the second and third pairs of the ventral hysterosomal setae are near the midline, and relatively close to the genital apparatus (Fig. 12 a–d). Nevertheless, it is most likely that these taxa may be referred to the first group of pterolichoids and hypothesis 3 may be applied. It is quite possible that the close proximity of these setae to the midline is the result of a general elongation process of the body in these taxa. It is quite interesting to note that in some evolved genera of the Syringobiidae family, the coxal setae 3a have been moved posterior and apart and occupy the position posterior to the genital setae g (if hypothesis 3 is applied, of course) (Fig. 12 d). The alternative suggestion that setae 3a simply moved posterior along the median line toward the genital apparatus and substituted the genital setae g, while the latter setae have moved apart toward the trochanters III seems to be quite doubtful.

Three pterolichoid families, Crypturoptidae, Eusthatiidae, and Thoracosathesidae, must be discussed separately. In males of the family Crypturoptidae, the genital apparatus is significantly moved anterior, to the level of the sejugal area or even to epimerites I, and, therefore, it is quite difficult to establish homology of the three pairs of ventral hysterosomal setae with respective setae of other pterolichoids. The first and second pairs are very near to the genital apparatus, or both are slightly posterior it; only the third pair is significantly distant from the genital apparatus and situated in the posterior part of the coxal fields IV (Fig. 14 b, c). In females of Crypturoptidae the disposition of ventral hysterosomal setae (Fig. 14 a) is similar to that in other pterolichoid families with three pairs of ventral hysterosomal setae (Fig. 9 a–d). Comparing the chaetome in males of Crypturoptidae with that in other pterolichoides, it is absolutely reasonable to conclude that the third pair is the coxal setae 4a, and hypothesis 3 is most likely applicable here. The main question is the homology of the first and second pairs, namely, which pair is the coxal setae 3a, and which is the genital setae g? It is most reasonable to suggest that the genital setae moved together with the genital

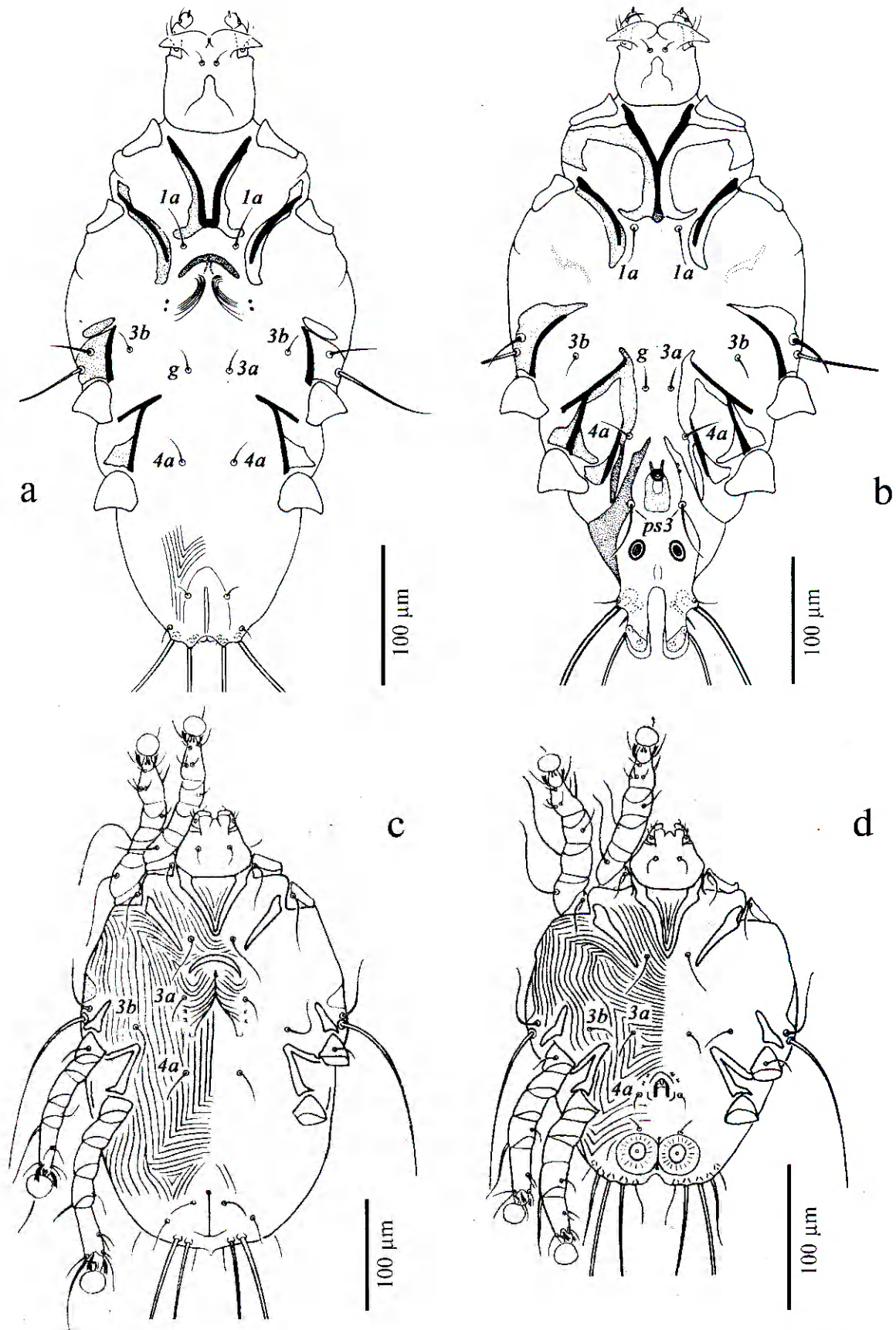


Fig. 13. Assignment of setal nomenclature for ventral hysterosomal setae in Pterolichoidea according to hypothesis 3; cases where some setae are absent.

a — *Eustathia cultrifera* (Robin) (Eustathiidae), female, b — same, male, c — *Epoplichus minor* (Megnin et Trouessart) (Pterolichidae, Epoplichinae), female, d — same, male. a, b — designations on the left side after Peterson et al. [1980], designation on the right side after Gaud and Atyeo [1996]. a, b — after Peterson et al. [1980], modified.

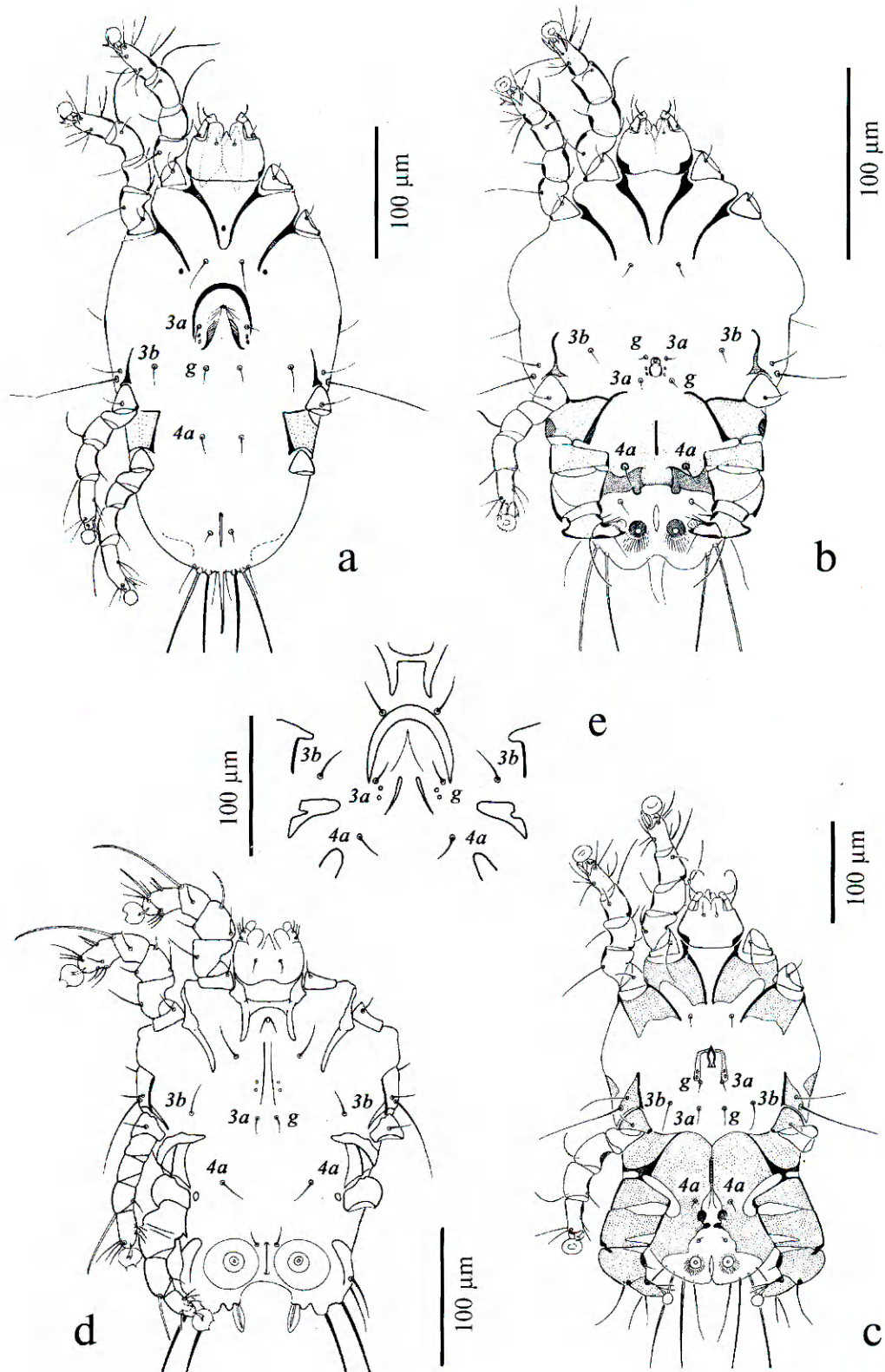


Fig. 14. Assignment of setal nomenclature for ventral hysterosomal setae in Crypturoptidae and Thoracosathesidae (Pterolichoidea) according to hypothesis 3; cases where some setae are absent or position of genital apparatus in males is greatly modified. a — *Allosathes anepiandrius* Gaud et al. (Crypturoptidae), female, b — same, male, c — *Crypturolichus forcipatus* (Trouessart et Neumann) (Crypturoptidae), male, d — *Thoracosathes thoracosathes* (Trouessart et Neumann) (Thoracosathesidae), male, e — same, female, central area of ventral idiosoma. a–c — designations on the left side after Gaud and Atyeo [1992], designations on the right side after Gaud et al. [1973]; d, e — designations on the left side after Atyeo [1992], designation on the right side according to alternative concept (see text). Modified drawings after: a–c — Gaud et al. [1973]; d, e — after Atyeo [1992].

apparatus, and finally reached the position anterior to the level of coxal setae *3a*. Therefore, in Crypturopodidae the first pair is the genital setae *g*, and the second pair is the coxal setae *3a*. This concept was applied to Cypturoptidae by Gaud and Atyeo [1996] (Fig. 14 b, c, left designations). The alternative suggestion that coxal setae *3a* had been moved to the median line and are situated closer to genital apparatus than the true genital setae *g*, while the latter setae are posterior to the genital apparatus and in some cases significantly distant from it, seems to be less reasonable (Fig. 14 b, c, right designations). Nevertheless, namely this alternative concept was originally used by the authors of the family [Gaud et al., 1973] (Fig. 14 b, c, right designations).

The family Eustathiidae is characterized by the reduction of one of three ventral hysterosomal setae in both sexes (Fig. 13 a, b). Peterson et al. [1980] proposed that the coxal setae *3a* (setae *c2* in the nomenclature used by these authors) have been lost in both sexes. Later, Gaud and Atyeo [1996] suggested that the genital setae *g* have been lost. Based on the topography of these ventral hysterosomal setae in males, it is most likely that the second pair, i.e. the genital setae *g*, is absent. Among the two remaining pairs, the most anterior pair occupies the level of the humeral shields, or trochanters III; therefore, it is, evidently, the setae *3a*. The posterior pair is situated anterior to the genital apparatus, and usually on the sclerotized inner margins of coxal fields IV; consequently, it is the coxal setae *4a*. This interpretation supports the theory presented by Gaud and Atyeo [1996]. However in Eustathiidae females, the anterior pair is situated significantly posterior to the egg opening (approximately at the level of the trochanters and of coxal fields III), and that suggests it is the coxal setae *3a* rather than the genital setae *g*. This interpretation corresponds to the concept of Peterson and coauthors [Peterson et al., 1980]. As shown above, the genital setae *g* in females are always the second pair of ventral hysterosomal setae and commonly situated posterior to the egg opening. So, we have a contradiction, which can be resolved in several different ways. If we insist that homologous setae have been lost in Eustathiidae, two conclusions may be drawn.

1. The setae *g* have been lost; the coxal setae *3a* occupy their normal position in males; in females, these setae are situated at the level of coxal fields III, because the egg opening has moved anterior, onto propodosoma, but the setae were not involved in this process. It is possible to object to

the latter suggestion by saying that in many other families of pterolichoids the egg opening has also moved anterior (Rectijanuidae, Thoracosathesidae), but setae referred to as *3a* always occupy the position at the level of the anterior end of the egg opening (Fig. 13 a, b, right designations).

2. The setae *3a* have been lost; in males, the setae *g* have moved anterior, to the level of epimerites III; in females, these setae occupy their normal position, posterior to the egg opening (Fig. 13 a, b, left designations).

If we admit that non-homologous pairs may be lost in males and females of Eustathiidae, it seems most reasonable to adhere to the concept proposed by Gaud and Atyeo [1996] in regard to males (loss of setae *g*), and to that of Peterson et al. [1980] in regard to females (loss of setae *3a*). To support this suggestion, it is possible to point out the non-synchronous loss of setae as observed in Analgoidea as an example. In several genera of Alloptidae (*Alloptes* Canestrini, 1879 and related genera), females may lose the setae *f2*, *ps1 ps2*, *g* in different combinations, while males of the same species retain all these setae.

Representatives of the family Thoracosathesidae are also lack of one pair of the ventral hysterosomal setae (Fig. 14 d, e), and almost the same speculations, as made above for the family Eustathiidae, may be drawn out in regard to this family. In males of the family Thoracosathesidae, the genital apparatus is greatly moved anterior, to the level of coxal fields I, and situated between epimerites I, while the two pairs of ventral hysterosomal setae retain far posterior, on hysterosoma (Fig. 14 d). It is quite difficult to decide, what setae have been lost in males, *3a* or *g*, and if hypothesis 3 is applied, it is clear only that the posterior pair occupying coxal areas IV is the coxal setae *4a*. However, based on the disposition of the ventral hysterosomal setae in females of Thoracosathesidae, it is most likely that the second pair (genital setae *g*) has been lost [Aty eo, 1992], because the first pair occupies the position lateral to oviporus and anterior to genital acetabulae (Fig. 14 e, left designations). Lacking of setae *3a* and moving of the genital setae *g* anterior, to the places normally occupied by setae *3a* in females of all pterolichoids (Figs. 9 a–d), seems to be less reasonable (Fig. 14 e, right designations). If we admit that the homologous pairs have been lost in males and females of Thoracosathesidae, it is possible to conclude that the anterior pair of the ventral hysterosomal setae in males is the setae *3a* in the first case (Fig. 14 d, left designa-

tions), or *g* (Fig. 14 d, right designations). The additional argument for the first case in regard to males: it is most probable to suggest that genital setae *g* moved together with the genital apparatus, than they were left far posterior to the genital apparatus and substituted the coxal setae *3a* in their places.

In contrast to Eustathiidae and Thoracosathesidae, the pterolichid genus *Epoplichus* Gaud, 1981 (Pterolichidae: Epoplichinae) may be given as the example of obvious loss of homologous setae within Pterolichoidea. Comparing the topography of ventral setae in both sexes of *Epoplichus* with that in related genera (for example *Pseudolichus* Atyeo et Gaud, 1992), it is clear that the genital setae *g* have been lost in both sexes (Fig. 13 c, d).

Finishing the discussion about homology between the ventral hysterosomal setae in feather mite superfamilies, it is possible to conclude that several problems still remain unsolved, and they trigger a number of different speculations. Nevertheless, it is possible to hope that they will, surely, be successfully solved in a future as a result of careful comparative investigations of chaetome ontogeny in representatives of each of these feather mite families and other astigmatid mites.

ACKNOWLEDGEMENTS

This discussion work was performed in the frame of the projects supported by the Russian Foundation for Basic Researches (Grant N 03-04-490072, 02-04-63000).

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