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Sixty years after “A review of the genera of the family Tydeidae” (Acariformes: Tydeoidea: Tydeidae)

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Original research

ABSTRACT

The goal of this paper is to present an overview of the genera of the prostigmatic mite family Tydeidae 60 years after the appearance of E.W. Baker’s seminal paper on the family (1965), and to define in systematic and scientific terms the genera within the superfamily Tydeoidea. Cumulative curves are given for genera, species and names. The number of morphospecies is estimated to be around 11,600 of which 3.72% have been described. Evolutionary plasticity and a new concept of the family are explored. The revised family is considered here to contain 31 genera and 3 non-nominal subgenera. Nomenclatural changes are noted in families, genera, subgenera and species: *Bakerlasiotydaeus* **n. gen.** (moved to Iolinidae, Tydaeolinae); *Neoafrotydeus* **n. gen.** (Tydeidae); *Neohomeotydeus* **n. gen**. (replaces *Homeotydeus* not in accordance with ICZN); *Afrotydeus*, junior synonym of *Tydeus* (**n. syn.**); *Paralorryia*, junior synonym of *Calotydeus* (**n. syn**.); *Pertydeus,* subgenus of *Tydeus* (**rest. comb.**); *Quadrotydeus*, subgenus of *Brachytydeus* (**rest. comb.**), *Eotydeus*, subgenus of *Brachytydeus* (**n. comb.**), *Bakerlasiotydaeus. krantzi* **n. comb**. (Iolinidae); *Tydeus nieukerkeni* (justified emendation) and *Homeotydeus formosus* (gender agreement). A table allowing the identification of female tydeid genera and subgenera is presented.

Keywords Iolinidae; dactyly; evolution; Tydeinae; Pretydeinae; Australitydaeinae
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> 述而不作　信而好古
> I transmit but do not innovate. Confucius, Analects 7: 1.
> Text and translation by Slingerland (2003).

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Introduction

Tydeidae was erected by Kramer (1877: 224) under the name Tydidae, a name not congruent with the guidelines of the International Code of Zoological Nomenclature (hereafter referred to as ICZN, or the Code) as a subfamily of Prostigmata proposed to accommodate the single genus *Tydeus* erected by Koch (1836). Previously, the genus *Tydeus* was placed in Eupodidae (Koch, 1850: 70). Later, *Tydeus* was still associated with eupodid mites by Canestrini (1892: 575) and Berlese (1925: 94). A first monograph treating the Tydeidae as a family including 14 genera, 4 subgenera, 69 determined and 13 undetermined species was provided by Thor (1933: 12) who placed them in Eupodoidea (together with Ereynetidae). Baker, in his seminal paper on the genera of the family Tydeidae, kept the sense used by Thor (Thorian sense), determined 15 genera and admitted that the family was “difficult to characterize” (Baker, 1965: 96). He

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divided the tydeids “into two groups, those with [seta] L[Lateral]$_2$ in the lateral position, and those with L$_2$ in line or nearly in line with the D[orsal] setae” (Baker, 1965: 98).

André (1979) divided the tydeids into seven subfamilies but kept the traditional Thorian sense. Subsequently and after numerous articles on species identifications, Kaźmierski (1996a, 1998a) presented the first approaches based on a phylogenetic analysis of Tydeinae and Pretydeinae.

André and Fain (2000) attributed a new meaning to the family they included in the superfamily Tydeoidea. This approach is adopted here. The superfamily included the Ereynetidae, Iolinidae, Tydeidae and Triophtydeidae. This classification with 4 families is also adopted. A diachronic view was given by André (2021, fig. 1).

Ecologically speaking, “the Tydeidae is perhaps the most common of all foliar mite families, and almost any tree, shrub, or liana that has not been treated by pesticides will have these mites on its leaves, stem, and bark” (Walter and Behan-Pelletier, 1999: 9). The relationship between tydeid mites and plants was recognized as early as the 1800’s, especially by botanists. One of the oldest records of this association is *Tydeus foliorum* Schrank, which was collected in Italy on the undersides of leaves, in moss, and in hay debris (Canestrini, 1896a: 233), north to Finland where it was frequently found in hay and grass (Nordenskiöld, 1900: 35). Lundström (1887: 9), Heinsius (1891: 197) and Ross (1904: 17) referred to the presence of *T. foliorum* in plant domatia. However, Abliz *et al.* (2014) mentioned them in passing in their publication for the Encyclopedia of UNESCO. Tydeids are pioneers in inner Antarctica (Janetschek, 1967) and are living in the Svalbard archipelago (Thor, 1933; Seniczak *et al.* 2020). They were collected from the sea level (Willmann, 1952) to the Himalayas (Momen and Solhøy; 1996; Chandra *et al.*, 2018).

In agroecosystems, Tetranychidae and Eriophyidae are famous due to the plant feeding problems they pose which were consequently clarified in compilations by Lindquist *et al.* (1996) and Ueckermann (2010). This is not the case of Tydeidae which forms a minor agricultural mite group even if Banks (1904) describing a new tydeid titled his publication as “Four new species of injurious mites” and stated that they were all “of considerable economic importance”. Subsequently, Tydeidae were treated as potential pests in major textbooks such as the “Mites Injurious to Economic Plant” by Jeppson *et al.* (1975), the “Agricultural Acarology: Introduction to Integrated Mite Management” by Hoy (2011), or the “Handbook of Mites of Economic Plants” by Vacante (2016). A famous exception is the species “*Lorryia formosa*” described by Cooreman (1958) (see the section on Inadequately described taxa). However, the status and function of Tydeidae as pests, beneficials, predators or alternate prey, are beyond the scope of this paper.

In food and stored products, Tydeidae were not even illustrated by Smiley (1987) and only 3 tydeid species were described from stored grain by Momen and Sinha (1991). However, they may be locally significant as in a chocolate production system with 55% of the mites collected (Silva *et al.*, 2024).

In medical and veterinary sciences, Tydeidae are also unimportant and not cited in the reviews by Mullen and OConnor (2019) and Lynn *et al.* (2024). A notable exception is *Tydeus molestus* described by Moniez (1889, 1894) in the garden of a Belgian farm and their impact on people. Analogous dermopathies produced by this mite or a similar species were described in an Italian school by Principato *et al.* (2008) and Principato and Scriboni (2009).

The systematics of the family are sometimes confusing, especially to beginners. Even a recent species such as *Quadrotydeus sleipneri* described by Momen and Lundquist (1996) has been assigned to two other genera: *Lorryia* (Kaźmierski, 1998a: 327) and *Brachytydeus* (Khaustov and Khaustov, 2023: 268). The beginners are still more embarrassed by the double assignation, in the same publication, of *sleipneri* to *Quadrotydeus* and to *Brachytydeus* (Silva *et al.*, 2016: 25, 34). This double assignation recalls that Dugès’ *caudatus* was simultaneously treated as a Tenuipalpidae and as a Tydeidae (André, 2011). “Neglect” for literature, divergent interpretations or contradictory observations also lead to confusion: *Afrotydeus* was erected by Baker (1970) as subgenus of *Tydeus* to accommodate three species, *munsteri, kenyensis*, and *meyerae*, which exhibit three different leg chaetotaxies. The world catalog published by Silva *et al.* (2016) treated a genus, *Pseudolorryia*, previously synonymized with *Calotydeus* by André (2005: 995), and did not include the genus *Calotydeus*. The genera erected by Berlese are named after the name with "a" after the "d" (*Lasiotydaeus*, *Melanotydaeus*) contrarily to *Stylotydeus* erected by Thor, Berlese even wrote *Tydaeus* instead of *Tydeus* in his publications and in his collection. This misspelling is sometimes found in recent articles. A last example concerns the coexistence of several designation systems based on location and a notation system founded on idionymy such as that developed by André (1980), which can be confusing as deplored by De Vis *et al.* (2024: 1097).

Quite simply, this paper aims at presenting an overview of tydeid genera sixty years after the seminal paper on the family Tydeidae presented by Baker (1965) and at defining them in a systematic and scientific way within the superfamily Tydeoidea, even if the superfamily is considered paraphyletic (Szudarek-Trepto *et al.* 2022).

Materials and method

This article treats extant morphospecies (i.e. species based on morphological criteria) described until 30 June 2024. Tydeid species described later in 2024 are not included (e.g. *Brachytydeus turkiyensis* described by Altunç *et al.*, 2024). The notation system proposed by André (1981b) is used only for apoteles and tarsi, a designation system is applied elsewhere.

A first database (1760 lines x 12 columns) was provided by the Integrated Taxonomic Information System (ITIS), namely by David Nicolson and Geoffrey D. Ower who were developing a web crawler for Tydeoidea. Their basic database was updated and completed, e.g. the number of combinations.

Other data are essentially based on personal data and bibliographical references (books, articles, review papers) on Tydeoidea taxonomy and on the database in the Wikispecies platform (André, 2021). Pertinent works were also consulted, such as monographs, books and catalog: Thor (1933), Baker and Wharton (1952), Baker (1965), André (1980), Kaźmierski (1998a) and Silva *et al.* (2016).

To avoid confusion, special attention is given to genera and their type species. For instance, *Lorryia cumbrensis* Baker, 1944 is the type species of the genus *Paralorryia* erected by Baker (1965). André (1980: 119) placed it in a new genus he called *Homeotydeus*, a nomenclatural act not in conformity with ICZN. Similarly, André (1980: 128) placed *Tydeus munsteri*, the type species of *Afrotydeus*, in a new genus he called *Orthotydeus* (type species: *T. goetzi*). Again, this fails to meet the rules of ICZN.

At the generic level, only meristic characters were considered, i.e. counts of discrete serially homologous structures (Lawing *et al.* 2008). Roughly, this corresponds to the presence/absence of idionymic characters outlined by Grandjean (1952). Diagnoses based on meristic characters were quite unusual before Baker's (1965) seminal paper and some genera were defined mainly by ornamentation. Although ornamentation may be a key character to delineate species (see figs 25-27 by Momen and Lundqvist, 1996), currently it does not provide adequate support at the generic level.

To determine the number of genera and species, *nomina novae* and replacement names were not retained. Similarly, misspelled names (e.g. *Australotydeus* instead of *Australotydaeus*) and specific epithets with no gender agreement (*formosa* instead of *formosus*) were not included in this publication. New combinations and revised diagnoses were likewise not included. Species with agronomical interests were considered so when they were described from an agroecosystem foliage or trunk, a statement such as "from soil samples of mango orchards" was not sufficient. *Incertae sedes* (e.g. species in which the phanerotaxy is not described in the original publication and in subsequent publications) were also counted.

The slopes, *m*, indicated in figure 3 were calculated the usual way: $m = (y_2 - y_1)/(x_2 - x_1)$ where y and x are the coordinates of the two end points of the line segment.

Results

List of genera excluded from Tydeidae

Genera initially described in Tydeidae but transferred later to other families include (in alphabetical order):

Genus transferred to Paratydeidae: *Scolotydaeus*.

Genera transferred to Triophtydeidae: *Apotriophtydeus*, *Edbakerella*, *Meyerella*, *Pretriophtydeus*, *Pseudotriophtydeus*, *Stenipedis*, *Teletriophtydeus* and *Triophtydeus*.

Genus transferred to Ereynetidae: *Pseudotydeus*.

Genera transferred to Iolinidae: *Aesthetydeus*, *Andretydaeolus*, *Apopronematus*, *Coccotydaeolus*, *Coleotydeus*, *Homeopronematus*, *Metapronematus*, *Metatydaeolus*, *Microtydeus*, *Naudea*, *Neonaudea*, *Neopronematus*, *Oakvillea*, *Parapronematus*, *Paratriophtydeus*, *Pausia*, *Primotydeus*, *Proctotydaeus*, *Pronecupulatus*, *Pronematulus*, *Pronematus*, *Pseudopronematulus*, *Reckitydeus*, *Tydaeolus* and *Tyndareus*.

List of genera and subgenera of Tydeinae

In the Linnaean system of nomenclature, the generic name is part of the Latin binomial attributed to all species, and therefore appears in every scientific paper dealing with living beings; it also gives this name an important role in systematics, certainly much more important than that of the names of higher taxa (Dubois, 1988: 15-16).

A partial and diachronic view of tydeine genera and subgenera is given in Figure 1. The current number of generic names amounts to 45 among which two are replacement names. In case of homonymy, replacement names are systematically appended to the replaced name (*Kuznetsovtydides* for *Tydides, Kuznetsovia* for *Venilia*) but they are listed hereafter. In contrast, synonymic genera, junior and senior synonyms, are drawn separately (e.g. *Quadrotydeus* and *Brachytydeus*). Most synonymies are not based on types (homotypic synonymy) but result from a comparison of data recorded in the literature (Fig. 1). Genera are listed hereafter in alphabetical order, except *Tydeus* the type genus. The number of component species (possibly before synonymization) potentially followed by the number of *species inquirendae* is indicated between square brackets.

(1) *Tydeus* [58+46]. The history of the genus is complex and convoluted and summarized by André (2005). The type species designated by the International Commission on Zoological Nomenclature (ICZN. 2008) is *Tydeus spathulatus* Oudemans, 1929 (consequently, it is also the type species of the family and superfamily).

(2) *Acanthodides* [1]. Monospecific genus erected by Kaźmierski (1996b). The type species is *A. jarema* by original designation.

(3) *Afridiolorryia* [3]. Genus erected by Kaźmierski (1996b). The type species, *Lorryia africana* Baker, 1965, was designated in the original publication.

(4) *Afrotydeus* [5]. It was erected by Baker (1970) as subgenus of *Tydeus* to accommodate three species: *munsteri*, *kenyensis*, and *meyerae*. These three species exhibit three different leg chaetotaxies. The type species designated by Baker (1970: 165) is *Tydeus munsteri* and not *A. kenyensis* as reported by André (1980: 107), Kaźmierski (1998a: 354) and Silva *et al.* (2016: 8). The species described by Meyer and Ryke (1959) and studied by André (1980: 126) and by Ueckermann and Grout (2007) has 6 genitals [and not 4 as noted by Baker (1970: 164)] and exhibits the same phanerotaxy as the nominal subgenus *Tydeus*.

(5) *Andrelorryia* [1]. This genus was erected by Khaustov (2022). Type species: *A. hajiqanbari* by original designation.

(6) *Apolorryia* [1]. Genus described by André (1980) with *Lorryia congoensis* Baker, 1970 as type species by original designation.

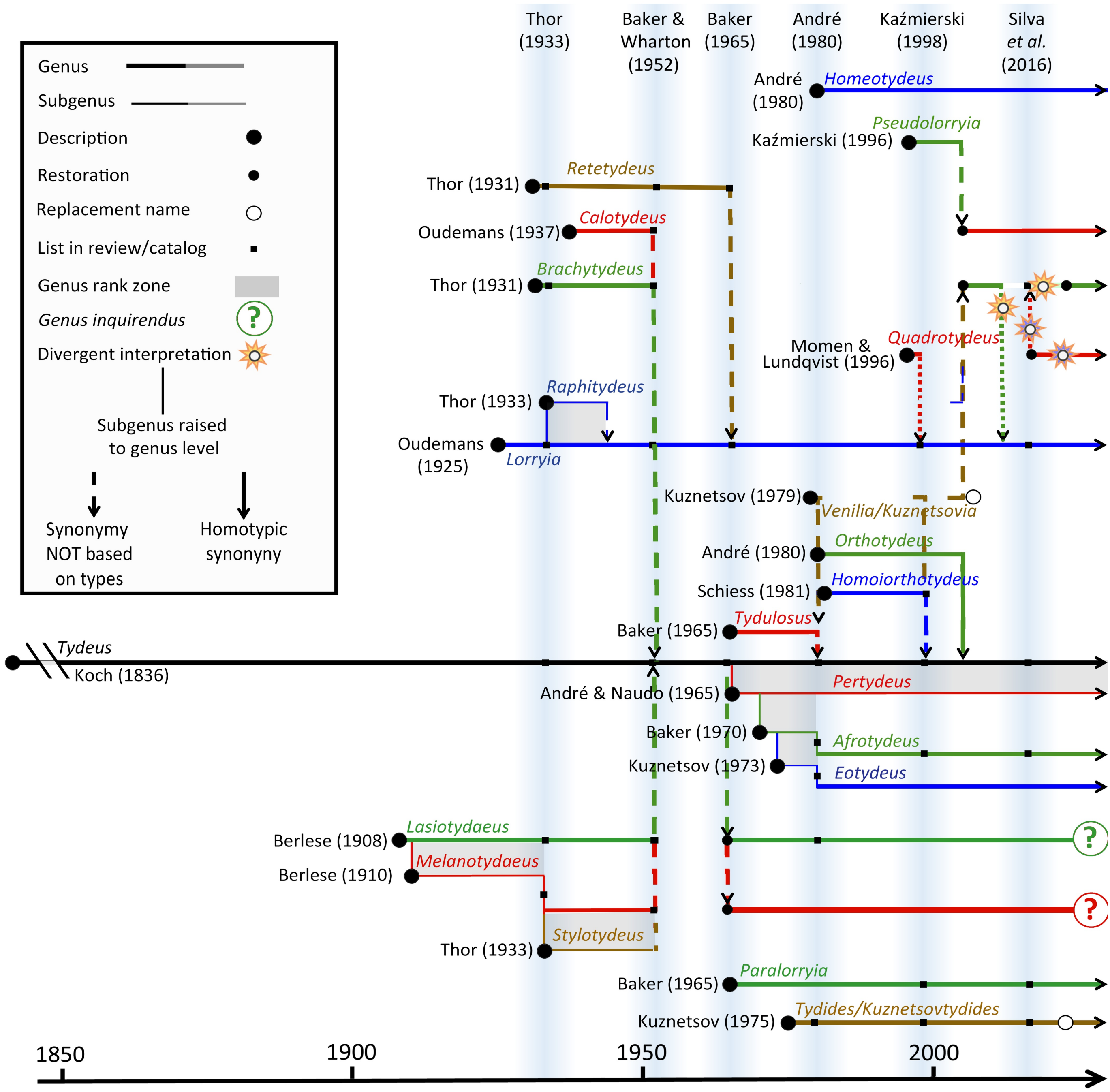

Figure 1 . Diachronic view of old genera and subgenera described in Tydeinae. Only formal synonymies are indicated, not the new combinations of type species.

(7) *Brachytydeus* [220+9]. The genus was erected by Thor (1931) with *Tydeus cruciatus* as the type species. The type species was redescribed by André (2005) in Oudemans' collection. Synonymized with *Tydeus* by Baker and Wharton (1952: 191) and by Baker (1965: 99). The genus was not listed by André (1980) and by Kaźmierski (1998a). It was restored by André (2005: 995) and catalogued by Silva *et al.* (2016: 9). Roughly, *Lorryia* sensu Kaźmierski corresponds to *Brachytydeus* (André, 2005: 995; Tempfli *et al.*, 2015: 944; Akbari *et al.*, 2015a: 424).

(8) *Calotydeus* [15+4]. The genus was erected by Oudemans and the type species is *Calotydeus croceus* by original designation (Oudemans, 1937: 922). Synonymized with *Tydeus* by Baker and Wharton (1952: 191), synonymization repeated by Baker (1965: 100). The genus was not listed by André (1980), Kaźmierski (1998a) and Silva *et al.* (2016) but was restored by André (2005: 995, 998). Among other species, the genus comprises the type species studied by Oudemans and three species described by Baker (namely *arthurbakeri*, *cumbrensis*, *shawi*). *Pseudolorryia* was synonymized with *Calotydeus* by André (2005: 995). A neotype from Oudemans' collection was selected by André (2005: 996).

(9) *Edlorryia* [1]. The type species by original designation of the genus erected by Kaźmierski (1996b: 201) is based on a unique specimen of Baker (1968), *Lorryia fundadorensis*, which is a deutonymph the chaetotaxy of which was partly published but completed by Kaźmierski (1996b: 201).

(10) *Eotydeus* [1]. Subgenus erected by Kuznetsov (1973) after study of Crimean specimens and raised to full genus rank by André (1980: 113) after examination of a Canadian specimen. Not listed by Kaźmierski (1998a) and Silva *et al.* (2016). The type species, *Tydeus* (*Eotydeus*) *mirabilis*, was assigned to *Lorryia* by Kaźmierski (1998a: 336) and to *Brachytydeus* by Silva *et al.* (2016: 19).

(11) *Homeotydeus* [2]. Genus erected by André (1980: 116–117) but without fixing a type species, which did not accord with Art. 13.3 of ICZN ("To be available, every new genus-group name published after 1930 … must … be accompanied by the fixation of a type species in the original publication"). Another discrepancy with the code (the inclusion of the type species of another genus) was outlined previously. Genus treated by Kaźmierski (1989). The 3 species described by Baker (namely *arthurbakeri*, *cumbrensis*, *shawi*) were transferred to *Calotydeus* by André (2005: 995, ambiguous remarks), the two Belgian species have a seta on coxa I and remained in the so-called genus. Synonymized with *Calotydeus* by André (2021: 1026).

(12) *Homoiorthotydeus* [1]. Genus proposed by Schiess (1981: 84) and synonymized with *Tydeus* by Kaźmierski (1998a: 342).

(13) *Idiolorryia* [2]. The type species of the genus erected by André (1980: 117) is *Lorryia macquillani* Baker, 1968, by original designation.

(14) *Kenlorryia* [1]. Monospecific genus described by Kaźmierski (1996b) with *Kenlorryia masaii* as type species by original designation.

(15) *Krantzlorryia* [1]. Monospecific genus erected by André (1980: 117) with *Lorryia grewia* Baker, 1968 as type species by original designation.

(16) *Kuznetsovia* [7]. Replacement name proposed by Kammerer (2006: 269) for *Venilia*, name already used for molluscs, insects, birds… Type species: *Paralorryia liberta* Livshitz, 1973. *Venilia* is a junior synonym of *Tydeus* according to André (1980: 154) or junior synonym of *Brachytydeus* according to André (2005: 995). Senior homonym of *Kuznetsovia*, replacement name advanced by Doweld (2016) for a Crustacea.

(17) *Kuznetsovtydides* [1]. Replacement name proposed by André (2021: 1030) for *Tydides*, name already used for insects. The genus was erected by Kuznetsov (1975) with *Tydides ulter* Kuznetsov, 1975 as type species by original designation.

(18) *Lasiotydaeus* [?]. First, monospecific genus erected by Berlese (1908: 15) with *Lasiotydaeus glycyphaginus* as type species. Descriptions are short: 6 lines for the genus, 3 lines for the species collected in Florence (Italy). The prodorsum illustrated by Berlese (1910: plate 18, fig. 6) has only 3 pairs of setae and it is difficult to conclude if it is pro- or recurved; however, the three setae are in line as in *mammilaris* (fig. 8, prodorsum recurved) and their alignment contrasts with the adjacent figure (fig. 7) in which the prodorsum is procurved with 4 setae arranged in a zigzag. Lastly, the dorsal opithosomal pattern drawn on that figure is simple, it consists of several transverse rows of 4 setae each and shows no trace of the dorsal migration of the second lateral setae (his L_2) evoked by Baker (1965). It was divided in 2 subgenera by Berlese (1910: 211), the nominal subgenus with

2 species and *Melanotydaeus* with 5 species. The genus was synonymized with *Tydeus* by Baker and Wharton (1952: 191; with a question mark). The genus—monosubgeneric—was restored by Baker (1965: 101) but was based on a Californian species (*L. krantzi*). The prodorsum of the Californian species described by Baker (1965: 101-102) and André (1980: 118) is procurved, the opithosomal pattern is different from that observed in tydeid mites, the tarsus I has 12 setae (vs 8 in Tydeinae), the Californian mite is not congeneric with the Italian type species (which seems to be a real Tydeidae even if it is impossible to know what the genus actually is) and appears to be an Iolinidae Tydaeolinae *genus inquirendus*.

(19) *Lorryia* [1]. Monospecific genus erected by Oudemans (1925) with *L. superba* as type species. The very short description of the initial paper was completed in a subsequent article (Oudemans, 1928a). The whole story is reported by André (2023). The genus was not listed by André (1980). The holotype and unique specimen of the type species is lost. Monospecific and, even recently, confused or synonymized with *Brachytydeus* (e.g. Mondin *et al.*, 2016; Khaustov *et al.*, 2020; Nuvolini *et al.*, 2020)

(20) *Melanotydaeus* [?]. *Melanotydaeus* was first described as a subgenus of *Lasiotydaeus* (Berlese, 1910: 211) and was raised to full generic level by Thor (1933: 48). It was divided into two subgenera, *Melanotydaeus* and *Stylotydeus* and synonymized with *Tydeus* by Baker and Wharton (1952: 191). It was restored by Baker (1965: 102) but was not keyed out. “The placing of *Melanotydaeus* as a synonym of *Tydeus* by Baker and Wharton must at present be considered to be in error” commented Baker (1965: 102) who concluded “The type, in the Berlese collection, is in extremely poor condition, and it is impossible to know what the genus actually is”. *Genus inquirendus*.

(21) *Melissotydeus* [3]. Genus erected by André (1985a: 244) with *M. macrosolenus* as type species by original designation.

(22) *Metalorryia* [7]. Genus advanced by André (1980: 118) with *Lorryia armaghensis* Baker, 1968 as type species by original designation.

(23) *Momenia* [1]. Genus proposed by Kaźmierski (1996b) with *Tydeus longichelus* Momen & El-Bagoury, 1989 as type species by original designation.

(24) *Neoapolorryia* [5]. Genus erected by El-Bagoury and Momen (1990) with *N. aegyptica* as type species by original designation.

(25) *Neolorryia* [3]. Genus advanced by André (1980: 127) with *Retetydeus boycei* Baker, 1944 as type species by original designation.

(26) *Nudilorryia* [6]. Genus erected by Kaźmierski (1996b) with *N. paraferula* as type species by original designation.

(27) *Orfareptydeus* [1]. Monospefic genus erected by Ueckermann and Grout (2007) for *O. stepheni*, type species by original designation.

(28) *Orthotydeus* [?]. Genus erected by André (1980: 127–128) with *Tydeus goetzi* as type species by original designation. However, André (1980: 128) mistakenly placed *Tydeus munsteri*, the type species of *Afrotydeus*, in *Orthotydeus*. Kaźmierski (1989) proposed a new combination, *Lorryia*. The genus was synonymized with *Tydeus* by André (2005: 996).

(29) *Paralorryia* [5]. Genus erected by Baker (1965) to receive Tydeinae with longitudinal striae between setae D_2. Type species by original designation: *Lorryia cumbrensis* Baker, 1944. Kaźmierski (1989) proposed a new combination. The genus was listed by Kaźmierski (1998a: 340) and by Silva *et al.* (2016: 32) (Fig. 1).

(30) *Perafrotydeus* [1]. Monospecific genus proposed by André (1980: 142) with *Tydeus* (*Afrotydeus*) *meyerae* Baker, 1970 as type species by original designation.

(31) *Pertydeus* [4]. This subgenus of *Tydeus* erected by André and Naudo (1965) and recognized by Baker (1970: 164). It was not listed by André (1980), Kaźmierski (1998a) and Silva *et al.* (2016) (Figure 1). The type species by original designation, *Tydeus schusteri*, was assigned to *Lorryia* by Kaźmierski (1998a: 336) and to *Brachytydeus* by Silva *et al.*

(2016: 24). No formulae were given in the description but the original figure 3 allows to identify the mite as belonging to the genus *Tydeus* (Fe II with 2 setae, Fe III with a single seta).

(32) *Pseudolorryia* [11]. The genus was erected by Kaźmierski (1989) and synonymized with *Calotydeus* by André (2005: 995). Type species: *P. edwardbakeri* by original designation.

(33) *Quadrotydeus* [1]. Monospecific genus advanced by Momen and Lundqvist (1996), synonymized with *Lorryia* by Kaźmierski (1998a: 293). The genus is listed by Silva *et al.* (2016: 34) but the type species, *Q. sleipneri*, was assigned to *Quadrotydeus* on page 34 and to *Brachytydeus* on page 25. The type species by original designation, *Q. sleipneri*, was assigned to *Brachytydeus* by Khaustov and Khaustov (2023: 268).

(34) *Quasitydeus* [2]. Genus erected by Kaźmierski (1996b) with *Tydeus* (*T.*) *ricensis* Baker, 1970 as type species by original designation.

(35) *Raphitydeus* [1]. Monospecific subgenus of *Lorryia* erected by Thor (1933: 54) for *Lorryia* (*Melanotydaeus*) *raphignathoides* Berlese 1910, type species by monotypy. Division not accepted by Baker (1944: 215) and recalled in Baker (1968: 987). Again, synonymized with *Lorryia* by Baker (1965: 105) and with *Brachytydeus* by André (2005: 995).

(36) *Retetydeus* [5]. Genus erected by Thor (1931) with *R. catenulatus* as the type species. Last used in mite descriptions by Baker (1944) for *boycei* and *doddsi*. The genus was listed—for the last time!—by Baker and Wharton (1952: 192), with *catenulatus* as type species. A synonymization with *Lorryia* was advanced by Baker (1965: 105). Although the type species, *catenulatus*, was never redescribed from Norway, it was included in the genus *Brachytydeus* by Silva *et al.* (2016: 13). The specimens of *R. viviparus* studied by Grandjean (1938) belong to *Brachytydeus*.

(37) *Stylotydeus* [2]. Subgenus erected by Thor (1933: 50) and synonymized with *Tydeus* by Baker and Wharton (1952: 191). No type species designated. The two component species (*brevistylus* and *styliger*) are *species inquirendae*.

(38) *Tydides* [1]. Monospecific genus erected by Kuznetsov (1975) for *T. ulter*. Junior homonym of the genus *Tydides* Stål, 1865 (Insecta, Reduviidae). Replacement name: *Kuznetsovtydides* provided by André (2021: 1030).

(39) *Tydulosus* [4]. The genus was erected by Baker (1965: 103) for species with a basket-weave pattern. The type species designated by Baker, *Tydeus granulosus* Canestrini, 1886a, is a *species inquirenda* and has no type. Synonymized with *Tydeus* by André (1980: 154). The species initially assigned to *Tydulosus* are included in *Brachytydeus* and *Tydeus* by Silva *et al.* (2016).

(40) *Venilia* [7]. Genus erected by Kuznetsov (1979) comprising 7 species reviewed by Kaźmierski (1981). Junior synonym of *Tydeus* according to André (1980: 154), junior synonym of *Lorryia* according to Kaźmierski (1989) and junior synonym of *Brachytydeus* according to André (2005: 995). Junior homonym of a mollusc, successive replacement names: *Kuznetsovia* and *Kuznetsovvenilia*. Type species: *Paralorryia liberta* Livshitz, 1973.

Genera in Australotydaeinae and Pretydeinae

(41) *Australotydaeus* [1]. Monospecific genus proposed by Spain (1969) for *A. kirstenae*, type species by original designation.

(42) *Novzelorryia* [1]. Monospecific genus erected by Kaźmierski (1996b) for *N. deserta*, type species by original designation.

(43) *Prelorryia* [2]. Genus erected by André (1980: 142-143) with *Lorryia indonesiensis* Baker, 1970 as type species by original designation.

(44) *Pretydeus* [12]. Genus proposed by André (1980: 143) with *Lorryia kevani* Marshall, 1970 as type species by original designation.

(45) *Ueckermannia* [1]. Monospecific genus advanced by Kaźmierski (1996b) for *Paralorryia grewiae* Ueckermann, 1988, type species by original designation. The type species is described in Ueckermann and Smith Meyer, 1988: 46-47.

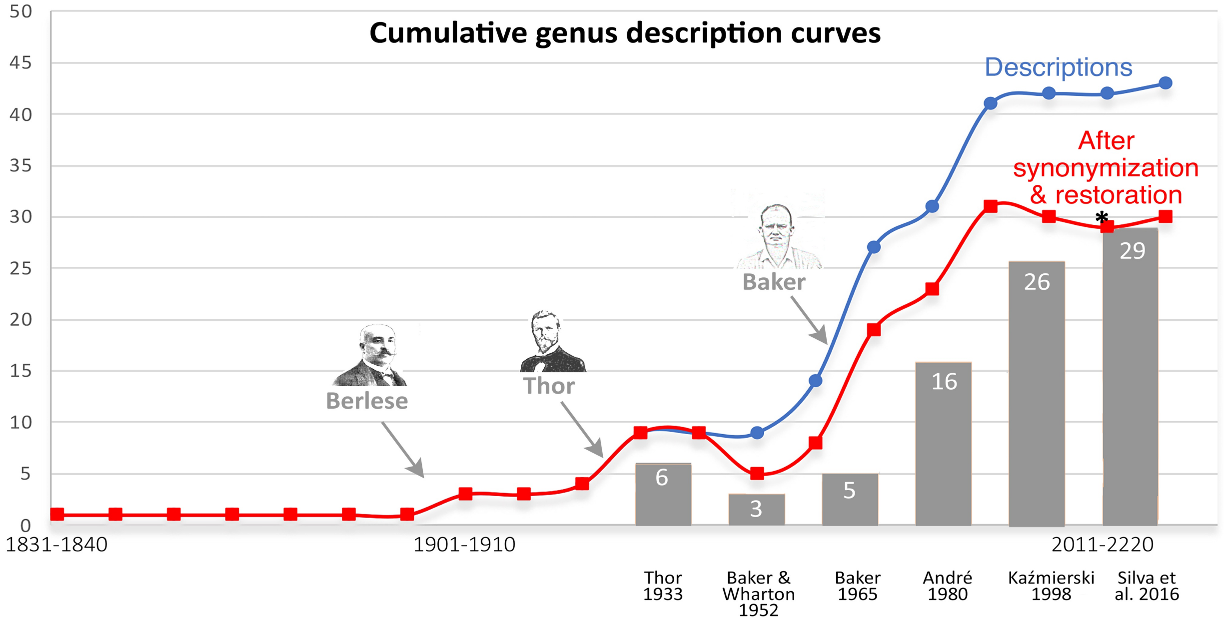

Figure 2 . Cumulative genus description curves in Tydeidae, with and without corrections following subsequent synonymies and restorations. Description years are grouped by decade. White numbers in histogram indicate the number of genera listed in the publications indicated below. Asterisk refers to the estimation by Zhang *et al.* (2011). The last point represents an incomplete decade (2021-2023). Subgenera are not included.

Number of genera in Tydeidae

The practical agreement which exists between specialists as to the delimitation of genera varies from one zoological group to another. In many groups, this agreement between specialists is poor, and this results in a great instability of the generic classification (Dubois, 1988: 16).

Figure 2 gives a histogram based on the monographs, books and catalog listed previously and two cumulative genus description curves since 1831. The first curve provides the number of all new genera and subgenera erected during each decade while the second takes into account synonymies and restoration. The maximum number of genera and subgenera described in Tydeidae is 43 (a total of 45 names – 2 replacement names). After synonymization and restoration, the current number of genera and subgenera in Tydeidae is 30 (Fig. 2). The instability evoked by Dubois (1988) is discernable through the gap between the two curves.

Depending on the curve selected, the number of genera at the beginning of the 2011-2021 decade amounts to 29-43 and is close to the estimation by Zhang *et al.* (2011: 130), 30 genera. Both curves apparently begin to flatten during the last 40 years.

Number of species in Tydeidae

A common approach to estimating the total number of extant species in a taxonomic group is to extrapolate from the temporal pattern of known species descriptions (Bebber *et al.* 2007). This perspective is not new in mites and was used by Wharton (1964) for mites and Trombiculidae and by André and N'Dri (2013) for mites and Tydeoidea. Yet, such an approach is not recommended due to the data weakness: only 433 tydeid species have been described, figure 3 shows the beginning of a logistic curve and there is no long-term trend *sensu* Edie *et al.* (2017).

Nevertheless, a turning point is apparent from figure 3 and is indicated by a double arrow. Both cumulative curves suggest a change in the description rate manifest trough the slopes estimated before and after the 1951-1960 decade. This is confirmed by the decade trend in species description with a maximum number of 83 species described in a single decade. The

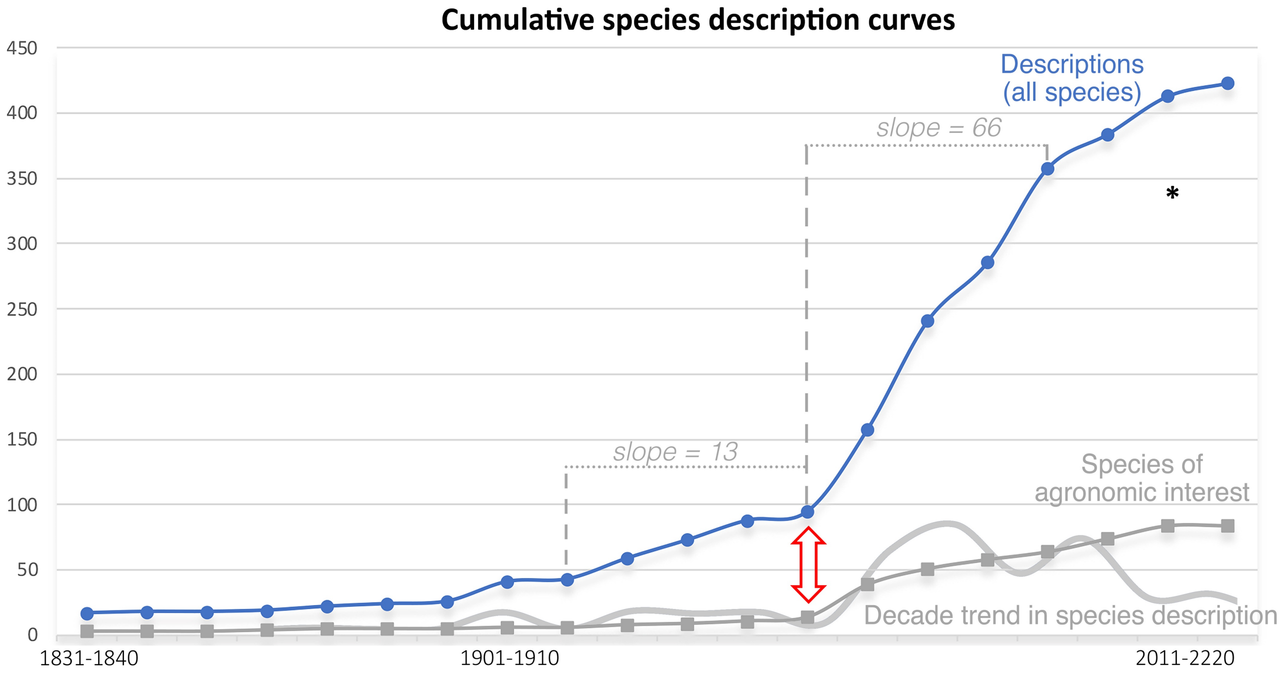

Figure 3 . Cumulative species description curves in Tydeidae and the decade trend in species description. Description years are grouped by decade. Asterisk refers to the estimation by Zhang *et al.* (2011). The last point represents an incomplete decade (2021-2023).

turning point coincides with the description of *Lorryia formosa* by Cooreman (1958) and seems to reflect the influence of agronomic practices.

However, another approach with a new "Pie of Life" was proposed by Larsen *et al.* (2017) and was based, concerning mites, on Walter and Proctor (2013). The number of described Acari species (including Acariformes and Parasitiformes) is approximately 55,000 (Krantz, 2009: 1). In such a context, 433 described tydeid morphospecies represent less than 1 percent of described Acari (0.79%). If assumptions of Larsen *et al.* (2017: 248; appendix 2 on animal richness, 10.2 million mite species including morpho- and cryptic species) are accepted, this yields 80,301 tydeid species. In the end, if a ratio of 5.9 cryptic species per morphologically based arthropod species is recognized (Larsen *et al.* 2017; appendix 1), this yields 11,638 tydeid morphospecies. 433 described tydeid morphospecies would then represent only 3.72% of estimated tydeid morphospecies in the world, less than the 10% recalled by Lindquist (2001: 55) for the eriophyoid fauna.

Obviously, there is no problem of species inflation as in mammals (Zachos *et al.*, 2013). Only 414 tydeid species had been described for the 2001-2010 decade vs 340 estimated by Zhang *et al.* (2011). The temporal pattern of known species descriptions was not modified by synonymies (4 cases) and restoration (2 cases).

Number of names in Tydeidae

Many binomina were given to a specific mite: 2.05 ± 0.76 for all tydeid species. A record is detained by the genus *Brachytydeus*. For instance, *zaheri* has five objective synonyms plus a replacement name (not counted): *Paralorryia* (original combination), *Brachytydeus*, *Kuznetsovia*, *Lorryia*, *Tydeus* and *Venilia*.

The number of binomina assigned to early described species is close to one (Figure 4). For instance, only a single combination has been used for *velox* Koch described in 1836:

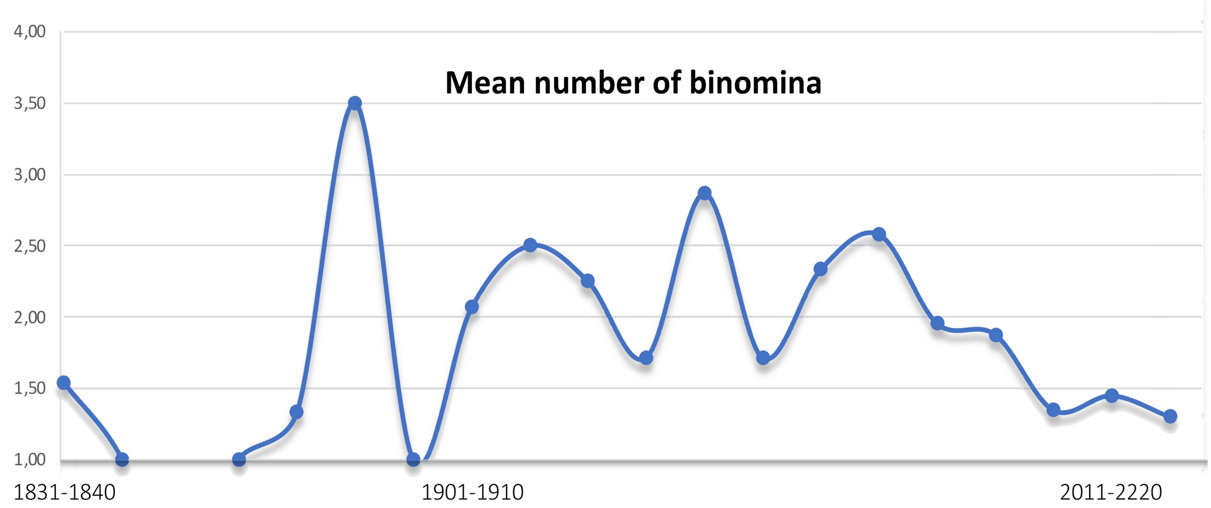

Figure 4 . Mean number of binomina of species according to the description year. Description years are grouped by decade. The last point represents an incomplete decade (2021-2023).

Tydeus velox. The same applies for recently described species, i.e. for *Brachytydeus altaicus* described by Khaustov and Khaustov in 2023, although there hasn't been enough time to propose objective synonyms to *B. altaicus*. There are large variations in between. A maximum value (3.5) is reached for species described in the 1881-1890 decade. For instance, there are 5 combinations for *granulosus* described by Canestrini (1886b): successively *Tydeus*, *Tydulosus*, *Venilia*, *Lorryia* and *Brachytydeus*. The trends observed in recent decades seems to indicate a decrease of subsequent combinations. The 17 species directly assigned to *Brachytydeus* were all described after 2008.

Toward a new concept of Tydeidae

In the Thorian sense, Tydeidae was "difficult to characterize" (Baker,1965: 96). In the modern sense, a key character advanced by André and Fain (2000) is the recurved prodorsum. This character is shared with Triophtydeidae but is very practical to recognize "real" Tydeidae in the old illustrations of Berlese and even in drawings of Baker (1965). The importance of the ecdysial cleavage line in Acariformes was discussed by Norton and Kethley (1994).

A second key character advanced by André and Fain (2000) is the presence of only two eye-spots vs three in Triophtydeidae. Those spots are silver granules not associated with a lens such as that found in Ereynetidae. As stressed by those authors, the presence of two eye-spots is not ambiguous. In contrast, their absence may refer to a nonobservance, i.e. the failure to observe them (e.g. the spots disappeared) or to a real absence (see Kaźmierski, 1989: 302; André and Fain, 2000: 416). The problem directly concerns *Australotydaeus kirstenae* in which no eye-spots have been reported and is still more puzzling when a population of *Tydeus* harbors 3 eyes as observed by André (1985b: 192) and recalled by André and Fain (2000: 412).

As noticed by André and Fain (2000: 437), the family Tydeidae is also characterized by the loss of eugenitals in females and a reduction of the cis-acetabular area. In the calyptostatic tritonymph drawn by Kuznetsov (1980: 1020, his fig. B), the 2 genital openings usually observed in tritonymphs are absent. This reduction is accompanied by the decrease of the chaetome, usually 6 genital setae on both sides of imagines. A decrease of genitals is observed in *Acanthodides*, *Apolorryia*, *Eotydeus*, *Momenia*, *Neolorryia*, *Pertydeus* and *Quadrotydeus*.

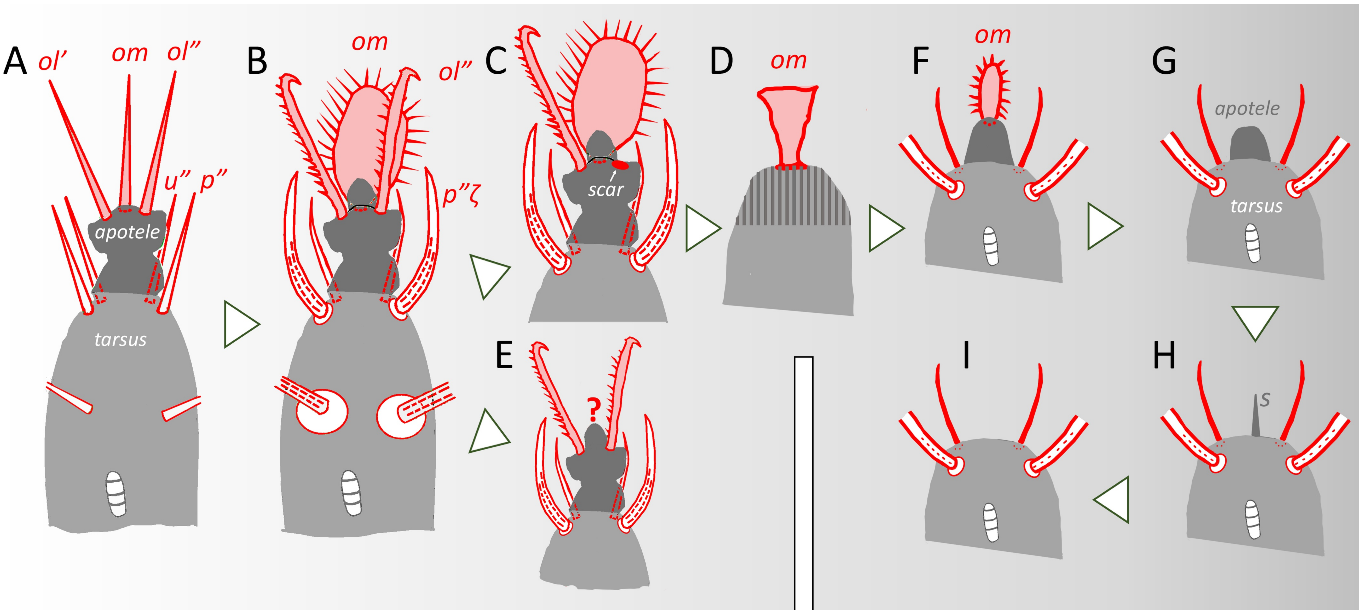

Figure 5 . From tridactyly to palpian evolution. A – Archetype; B – Tridactyly (André & N'Dri, 2013); C – Heterobidactly (Oudemans, 1925); D – Apotele fused (Kuznetsov, 1980); E – Homobidactyly (André, 2008, 2024); F – Monodactyly (Treat, 1970); G – Apotele vestigial (putative step); H – Apotele setiform (De Vis *et al.* 2024); I – Apotele absent (Knop & Hoy, 1983). Homologous structures have the same pattern. Birefringent structures are outlined (in red in electronic format). Most steps correspond to a species and an article indicated between brackets. A–E: legs I to IV; F–I: leg I only.

The absence of genitals was even observed in the calyptostasic tritonymph of *Brachytydeus* (Kuznetov, 1980). Similarly, there are 3 aggenitals (instead of 4) in *Apolorryia* and *Eotydeus*.

Such a reduction of genitals may be unilateral (occurring on one side of the body) as noticed by Momen and El-Baghouri (1994), Momen and Solhøy (1996), Momen and Lundquist (1996) and Kaźmierski (1989). The generic significance of this character was questioned by Kaźmierski (1989: 300-301) and the trait will be used to delineate subgenera only. Furthermore, the unilateral presence of 7 genitals reported by Momen and El-Baghouri (1994) and Momen and Solhoy (1996) demonstrates that two forces are governing the evolution of Tydeidae. On the one hand, the fluctuating asymmetry seems to be caused by random developmental accidents (RDA in Figure 6) not corrected by homeostatic mechanisms normally resulting in a perfect bilateral symmetry (Leponce *et al.*, 2001). On the other hand, Grandjean (1942) gave an evolutive significance to the unilateral changes he called vertitions (V in Figure 6) and governed by homeostatic mechanisms.

A last distinguishing trait, not evoked by André and Fain (2000), is the presence of at most 8 setae on tarsus I in all Tydeinae and Pretydeinae. Australotydaeinae has a special chaetotaxy with 10 setae on tarsus I and exhibits intermediate characters with other Tydeoidea. This counting is based on the designation system developed by André (1981b).

Other formulae are variable. The most frequent epimeral formula is (3-1-4-2). (3-1-4-3) has been observed in *Krantzlorryia*, *Pretydeus* and *Tyndareus.*

Evolutionary plasticity of Tydeidae

An evolutionary trait-based approach was selected by André (2023) to define the genus *Lorryia*. In this approach, Tydeidae anticipate the evolutionary traits found in other families of Tydeoidea.

For instance, the reduction of chaetotaxy of tarsus I and the dactyly observed in Tydeidae may be conceived as a vast evolutionary move leading to the fusion or loss of apotele I and the resulting palpian evolution of leg I observed in Iolinidae (Figure 5).

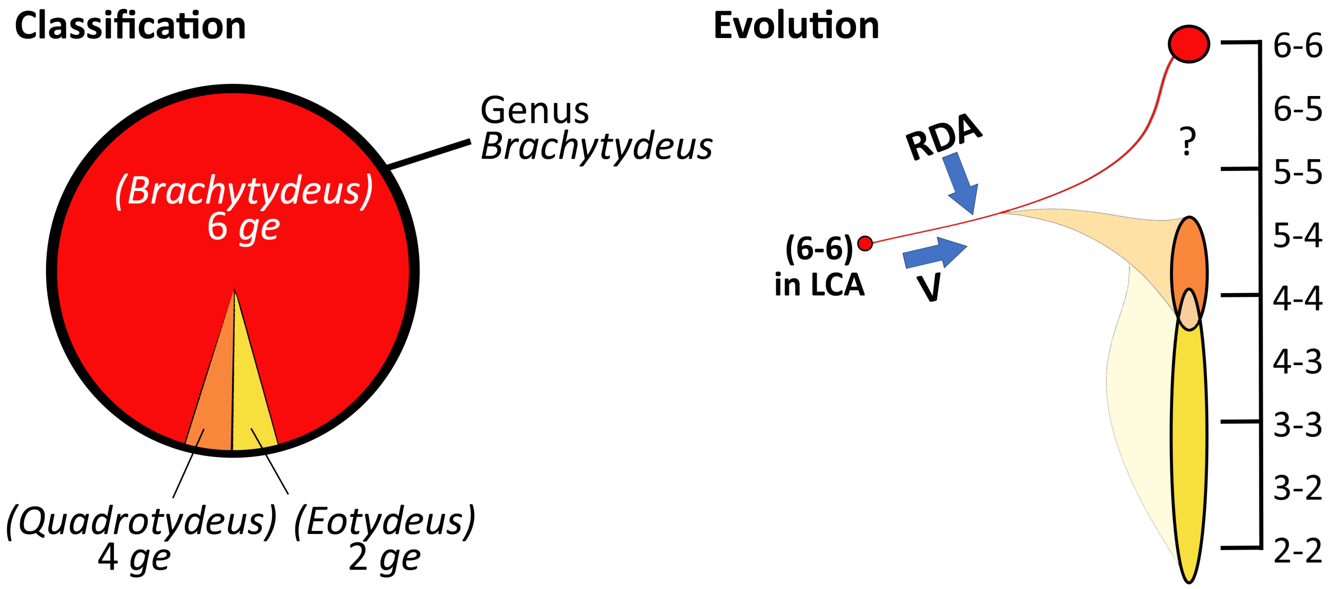

Figure 6 . Classification (left) and evolution (phylogram of genitals, right) of the genus *Brachytydeus* and its subgenera. LCA: least common ancestor; V: vertition; RDA: random developmental accident. Right scale: number of genitals on each hemibody from 6-6 to 2-2. The scenario retained postulates that (*Quadrotydeus*) forms a branch (*Eotydeus*)-(*Quadrotydeus*) arising from a common ancestor LCA and that (*Eotydeus*) arises from that branch. In another scenario, (*Quadrotydeus*) might be closer to (*Brachytydeus*) and forms a branch (*Brachytydeus*)-(*Quadrotydeus*) before which arises (*Eotydeus*). Either scenario is consistent with the classification proposed.

Another aspect of evolutionary plasticity of Tydeidae is shown by the reduction of the cis-acetabular area and the decrease of the chaetome which also anticipate the evolution of Iolinidae.

A further facet of evolutionary plasticity of Tydeidae is shown by the partly recessed solenidion, φI, observed in *Pretydeus*. It does not differ from the ereynetal organ of some ereynetid larva.

A last aspect of evolutionary plasticity of Tydeidae concerns the ontogeny. Apart from a calyptostatic prelarva, described and drawn by Kuznetsov (1980: 1020, his fig. A) and photographed by André and N'Dri (2013: 60, their fig. 50), the ontogeny of Tydeidae includes one six-legged larva (larviparity, drawn by Thor 1933: 52, his fig. 62) followed by four eight-legged stases: the protonymph, deutonymph, tritonymph and imago (♀and ♂). In other words, adulthood (sexual maturity) is observed in imagines only. Based on laboratory colonies (Brickill, 1958; Kuznetsov, 1980; Liguori *et al.* 2002; Hernandes *et al.*, 2006; Silva *et al.*, 2014), there is no missing stase as in spider mites (André and Van Impe, 2012) but the tritonymph can be reduced to a calyptostasis as presented and illustrated by Kuznetsov (1980: 1020, his fig. B). This recalls the intervening calyptostases observed in ereynetid Speleognatinae (Fain, 1972; André and Fain, 1991).

Nomenclatural acts

Nomenclatural acts (1) to (8) concern families, genera and subgenera, subsequent acts concern species.

(1) *Bakerlasiotydaeus* **new genus** Zoobank: 86ABB6B5-0AE1-4AE8-A7EB-6C105208B3D6
Lasiotydaeus krantzi is not a Tydeidae but an Iolinidae as noticed by Darbemamieh *et al.* (2016). The Californian species was described in detail by Baker (1965) and André (1980). Therefore, a new genus and a new combination are proposed: *Bakerlasiotydaeus* **new genus**. with *L. krantzi* as type species, and *B. krantzi* **n. comb**. The precise place of

Bakerlasiotydaeus within the Iolinidae is beyond the scope of this paper but, according to André (1980: 118), the Californian species is closely related to *Primotydeus* (Tydaeolinae).

(2) *Afrotydeus* and its type species, *Tydeus munsteri*, exhibits the same phanerotaxy as the nominal subgenus *Tydeus*. *Afrotydeus*, be it a subgenus or a genus, is thus considered a **junior synonym** of *Tydeus.* Topotypes or types of both type species were examined. Consequently, the original combination, namely *Tydeus munsteri*, has to be used again and any other combination must be set aside. *Tydeus (A.) meyerae* was moved to *Perafrotydeus* by André (1980: 142), the other species are placed in a new genus defined hereafter (act 4).

(3) Similarly, the type species of the genus *Paralorryia*, *cumbrensis*, has the same organotaxy (leg and idiosoma) as *croceus*, the type species of *Calotydeus*. Types of both species were examined. As a result, *Paralorryia* is thus considered a **junior synonym** of *Calotydeus*.

(4) *Neoafrotydeus* **new genus** Zoobank: 1EC6999B-930C-40AB-9AB7-4BF259A477CC
Neoafrotydeus **new genus** is erected with *kenyensis* as type species to accommodate *Tydeus* (*Afrotydeus*) *flabellifer*, *T.* (*A.*) *kenyensis*, *A. novaezealandiae*, *A. smileyi* and *A. zairensis*, species currently assigned to *Afrotydeus*, genus synonymized with *Tydeus* as noted above.

(5) *Neohomeotydeus* **new genus** Zoobank: CAAAE9E6-4DB5-441C-92CC-51B15227DB96
Homeotydeus was erected by André (1980) but is not in conformity with ICZN. The 3 species described by Baker (namely *arthurbakeri*, *cumbrensis*, *shawi*) have a seta on trochanter I and were transferred to *Calotydeus* by André (2005: 995, ambiguous remarks.). The other two species, namely *H. bipilis* and *H. formosus*, have a nude trochanter I and are accommodated in a **new genus**, *Neohomeotydeus* with *H. formosus* as type species.

(6) *Pertydeus* was described as a subgenus of *Tydeus* and exhibits the same leg chaetotaxy as the nominal genus *Tydeus*. The number of genitals is however 5 (vs 6 in *Tydeus*). *Pertydeus* thus re-established in its pristine state and restored as a subgenus of *Tydeus* (**rest. comb.**).

(7) Similarly, *Quadrotydeus* is considered to be a subgenus of *Brachytydeus* characterized by the same leg phanerotaxy but with only 4 genitals (**new comb.**).

(8) Similarly, *Eotydeus* is considered to be a subgenus of *Brachytydeus* characterized by the same leg phanerotaxy but with only 2 genitals as in the original description (**new comb.**).

(9) *Tydeus nieu(w)kerkeni.* André (2005) was naming the species after Dr Erik J. van Nieukerken, yet the name was published as *nieuwkerkeni*, an incorrect original spelling. Under art. 32.5 of ICZN, the correct spelling is emended to *nieukerkeni*. A "justified emendation" (Art. 33.2.2), if corrected under article 32.5, results in the same author and date as the original name.

(10) *Homeotydeus formosa*, the binomen used by André (1984), does not respect the gender agreement. The original combination corrected under art. 34.2 of ICZN is *Homeotydeus formosus* which is the type species of the genus *Neohomeotydeus*.

Table 1 shows that some genera are very close and that the difference may concern only a single seta: *Brachytydeus–Kuznetsovtydides* (seta on trochanter I), *Calotydeus–Tydeus* (seta on femur II). Table 1 also masks the within diversity of genera. For instance, chaetotaxy of leg II in *Idiolorryia* is displayed (6-2-1-3-0) while it has been observed a single seta on tibia. Variations in leg chaetotaxy was explored by Momen and Lundqvist (1993). Similarly, there are 4 or 5 genitals in *Neolorryia*, 2 to 4 in *Eotydeus*. Consequently, the division into subgenera is debatable due to the high variability of the number of genitals. *Edlorryia* based on a deutonymph, *Lasiotydaeus* and *Melanotydaeus* (*genus inquirendus*) do not figure in table 1.

Discussion

Chronic problems

It is important to distinguish chronic problems as those listed by Lindquist (2001) from problems specific to Tydeoidea. Language and cultural barrier: "phanere" is a word absent from the English dictionaries, unused in the manual of acarology edited by Krantz and Walter (2009) and covers, in acarology, setae and other setiform organs. Acarological terminology remains obscure and some chaetotactic formulae refer to all setiform organs, in whatever form. Systems of notation/designation for setae and other external structures are also a source of confusion as regretted by De Vis *et al.* (2024: 1097).

Table 1 . Traits of tydeid genera (♀ only) with epithet of the type species in square brackets. Genera are listed in alphabetical order, except *Tydeus* the type genus. Underlined values differ from that of observed in *Tydeus* (type genus). Leg I to IV: chaetotactic formulae on legs. S: leg solenidiotaxy. Cl.: Number of claws. Palp: chaetotactic formula on palp. G: number of genitals. **: Type of the type species examined. *: other species examined. Chaetotactic formulae of subgenera are not repeated. The table may be used as an identification key.

Genus + type species [epithet only]	Leg I	Leg II	Leg III	Leg IV	S	Cl.	Palp	G
TYDEINAE								
Tydeus [*spathulatus*]**	8-4-3-3-1	6-2-2-2-0	5-2-1-1-1	5-2-1-1-0	2	2	6-2-2	6
(*Pertydeus*) [*schusteri*]								5
Acanthodides [*jarema*]	8-4-3-3-1	6-2-2-3-0	5-2-1-2-1	5-2-1-1-0	2	2	6-2-1	3
Afridiolorryia [*africana*]	8-4-2-3-0	6-1-1-2-0	5-1-1-1-1	5-1-1-1-0	2	2	6-1-2	6
Andrelorryia [*hajiqanbari*]*	8-4-3-3-0	6-2-2-3-0	5-2-1-2-1	5-2-1-1-0	1	2	6-1-2	6
Apolorryia [*congoensis*]**	7-3-1-2-0	6-1-1-2-0	5-1-0-1-0	5-1-0-1-0	2	2	6-2-2	3
Brachytydeus [*cruciatus*]**	8-4-3-3-1	6-2-2-3-0	5-2-1-2-1	5-2-1-1-0	2	2	6-2-2	6
(*Quadrotydeus*) [*sleipneri*]								4
(*Eotydeus*) [*mirabilis*]*								2
Calotydeus [*croceus*]**	8-4-3-3-1	6-2-2-3-0	5-2-1-1-1	5-2-1-1-0	2	2	6-2-2	6
Idiolorryia [*macquillani*]**	8-4-2-3-0	6-2-1-3-0	5-1-1-2-1	5-1-1-1-0	1	2	6-1-2	6
Kenlorryia [*masaii*]	7-4-3-3-1	6-2-2-3-0	5-2-1-1-1	5-2-1-1-0	2	2	6-2-2	6
Krantzlorryia [*grewia*]**	8-3-2-2-0	6-2-1-2-0	5-2-0-1-1	5-2-0-1-0	2	2	6-1-2	6
Kuznetsovtydides [*ulter*]	8-4-3-3-0	6-2-2-3-0	5-2-1-2-1	5-2-1-1-0	2	2	6-2-1	6
Lorryia [*superba*]	?	?	?	?	?	1	2-2-2	6
Melissotydeus [*macrosolenus*]**	8-4-3-3-1	6-2-2-3-0	5-2-1-2-1	5-2-1-2-0	2	2	6-2-2	6
Metalorryia [*armaghensis*]**	8-3-2-3-0	6-2-1-2-0	5-2-1-1-1	5-2-1-1-0	2	2	6-1-2	6
Momenia [*longichelus*]	7-4-3-3-1	6-2-2-3-0	5-2-1-2-1	5-2-1-1-0	2	2	6-2-2	6
Neoafrotydeus [*kenyensis*]**	8-4-3-3-1	6-2-1-1-0	5-2-1-1-0	5-2-1-0-0	2	2	6-2-2	4
Neoapolorryia [*aegyptica*]	8-3-2-2-0	6-1-1-2-0	5-1-0-1-0	5-1-0-1-0	2	2	6-1-2	6
Neohomeotydeus [*formosus*]**	8-4-3-3-0	6-2-2-3-0	5-2-1-1-1	5-2-1-1-0	2	2	6-2-2	6
Neolorryia [*boycei*]**	8-3-2-2-0	6-1-1-2-0	5-1-0-1-1	5-1-0-1-0	2	2	6-1-2	5
Nudilorryia [*paraferula*]	8-4-3-3-0	6-2-2-3-0	5-2-1-2-1	5-2-1-1-0	2	2	6-2-2	6
Orfareptydeus [*stepheni*]	8-4-3-2-1	6-2-2-1-0	5-2-1-0-0	5-2-1-0-0	1	2	6-2-2	6
Perafrotydeus [*meyerae*]	8-4-3-3-1	6-2-2-1-0	5-2-1-1-0	5-2-1-0-0	2	2	6-2-2	6
Quasitydeus [*ricensis*]	8-4-3-3-1	6-2-2-3-0	5-2-1-1-0	5-2-1-1-0	2	2	6-2-2	6
PRETYDEINAE								
Novzelorryia [*deserta*]	8-3-2-3-1	6-2-0-3-0	5-2-0-1-1	5-2-0-0-0	3	2	6-2-2	6
Prelorryia [*indionensis*]**	8-4-2-3-1	6-2-0-3-1	5-2-0-1-1	5-2-0-0-0	2	2	6-2-2	6
Pretydeus [*kevani*]**	8-4-2-3-1	6-2-0-3-1	5-2-0-1-1	5-2-0-0-0	3	2	6-2-2	6
Ueckermannia [*grewiae*]	8-3-2-3-0	6-2-0-3-0	5-2-0-1-1	5-2-0-0-0	3	2	6-2-2	6
AUSTRALOTYDAEINAE								
Australotydaeus [*kirstenae*]**	10-5-3-5-1	6-2-3-3-1	5-2-1-1-1	5-2-0-2-0	2	2	6-2-2	6

Not included: *Edlorryia* (deutonymph), *Lasiotydaeus* and *Melanotydaeus* (*genera inquirenda*).

Figure 7 . The distribution of study sites of tydeid types between A – 1901 to 1920, B – 1951-to 1970, and C – from 2001 to 2020. The influence of Berlese (Italy) and Thor (Sweden) is apparent in A.

As their colleagues, acarologists who deal with Tydeoidea have a limited knowledge of global acarofauna. Even if the Eurocentrism apparent in Figure 7A tends to disappear later, some major areas have been little explored: Africa (no tydeid mite in the catalog by Mwase and Baker, 2006), Australia (Halliday (1998) does not cite a single identified species), China (only 27 determined species in Lin and Zhang, 2010: 54), Middle East (17 determined species in Kamali *et al.*, 2001: 150-152; only 1 in Halliday *et al.*, 2018: 133), North America (only 30 species in Beaulieu *et al.* (2019: 97)… This limited knowledge of Tydeidae may be perceived as a cognition still at a nascent stage (Stepanyan and Zarikian, 2024: 217). Another indicator of limited knowledge is the absence of recapture of atypical species described long ago: *Australotydaeus kirsteneae* described by Spain (1969) and *Lorryia superba* described by Oudemans (1925) but collected in 1923.

Lastly, molecular data are indicative of cryptic or undescribed species. Beaulieu *et al.* (2019: 97) cited only 30 tydeid morphospecies known from Canada against 217 species based on molecular data; i.e. morphospecies would represent at most 14% of all species living in Canada.

Objectivity and objective synonymies

Not only the "ancient" species are neglected, but also the types. The principle of typification states that any named taxon, in the family group, genus group or species group, has a name-bearing type which allows the application of the name of the taxon to be objectively applied. Yet, name-bearing types are rarely requested to be the reference object for a necessary redescription or an accurate identification. Most synonymies between genera are not based on the type material (Fig. 1). Synonymies may even result from synonymization without comments as done by Baker and Wharton (1952: 191) because the family had "been divided in the past into too many genera based on such characters as size, width, length of setae, type of setae, and presence or absence of eye spots." The absence of any explanations is also noticeable when Baker (1970: 163) proposed new combinations for species originally placed in *Tydeus*.

Whatever the sense attributed to objectivity through history (Daston and Galison, 2007; Latour, 2012), types in ICZN provide an objective reference for the allocation of a *nomen* to any taxon and designate objects (Dubois, 2011: 21).

Inadequately described taxa

Inadequately described taxa is another problem emphasized by Lindquist (2001) and rendered more complicated by the absence of redescriptions. Yet, Baker (1965: 95) already wrote that "it will be necessary to re-collect at type localities to determine the status of most European species". Most *Tydeus* described by Koch from Regensburg (Germany) were inadequately described, have never been redescribed and there is no neotype. *Tydeus breviculus* redescribed by Kaźmierski (1998a: 305) is based on Polish specimens, not on topotypes. Its synonymy with *Tydeus curtus* Berlese, 1910 is therefore suspect.

The first complete organotaxy was provided by Grandjean (1938), which means that earlier descriptions are seriously inadequate and concern 72 species (i.e. 17% of current species). Leg chaetotaxies published before Baker's (1965) seminal paper were quite unusual and such an absence concerns *ca* 95 species (22%). Redescriptions are exceptional (less than 1% of described species) and only include that of *Tydeus italicus* by Kaźmierski (1998a: 310–311) and those of *T. croceus* (L.), *T. cruciatus* Koch and *T. spathulatus* Oudemans by André (2005), all from Oudemans' collection.

Inadequate descriptions and the absence of subsequent redescriptions also concern important species such as "*Lorryia formosa*" first collected on citrus in Northern Africa. The original description did not mention the organotaxy of legs and did not illustrate several setae (P_2, H_1 or H_2), the reticulation pattern is just sketched in fig. 15. The chaetotactic formulae deduced from original figures (figs 7-10), I(6-3-2-2-0) II(6-2-2-2-0) III(5-2-1-1-0) IV(5-2-0-1-?), do not correspond to formulae of Table 1. What does *Lorryia formosa* authorem designate? Is it the same species as that described by Cooreman (1958)? *Metalorryia magdalenae* described by Gerson (1968), also with a reticulated pattern, was also collected from citrus in the same climatic zone; what are the differences with the species described by Cooreman (1958)?

A similar problem arises with *Tydeus kochi* Oudemans (1928b: 377) mentioned a species with bulbous short setae ("kolbige kurze Borste" in German) while Baker (1970: 170–171, his fig. 26) drew a species with nude setae said to be "of medium length, lanceolate, serrate". What does *Tydeus kochi* authorem designate?

Adequate (re)descriptions

"Ancient" species are often neglected. If the ornamentation (striation pattern, reticulation, basketweave…) is disregarded at the generic level, it is of paramount importance (together to the state, shape, length of setiform organs) to delineate species. A helpful system for such was proposed by Kaźmierski (1998a: 288-289). However, the ornamentation is difficult to represent with drawings and illustrates the problems encountered when we look back into the past with modern techniques and equipment (Ratcliff, 2009). In Akbari *et al.* (2015b), the habitus of *Tydeus shabestariensis* is illustrated both with a drawing (their figure 1) and with a photograph (their figure 3). The comparison of photos and line drawings revealed that dorsal body setae seem thicker and more serrated in drawings than in photos. Another example is provided by Ripka *et al.* (2013) who described several new species of arboreal Tydeidae from Hungary. They provided phase contrast photos for some species. The comparison of photos and line drawings again reveals some inadequacy of line drawings. The photo of *Lorryia sanctikingai* clearly illustrates rather thick and blunt-tipped dorsal idiosomal setae (their fig. 18) while line drawings (their fig. 15) suggest thin and pointed setae. This recalls the old debate between drawings and photographs in science. "But the 'photographic eye' does not approach the objects only in a more honest and unbiased way, it is often able to grasp them more directly and more sharply." ("Aber das 'photographische Auge' tritt an die Gegenstände nicht nur ehrlicher und vorurtheilsloser heran, es vermag dieselben auch vielfach unmittelbar genauer und schärfer zu erfassen.") advanced Fraenkel and Pfeiffer (1892: 1). Starr *et al.* (1896: vi) added: "But all such drawings are necessarily imperfect and involve a personal element of interpretation."

Photographs of the striation pattern in Tydeoidea was introduced by André and Ducarme (2003). In the future, adequate micrographs must be part of any (re)descriptions, be they phase contrast micrographs (e.g. Escobar-Garcia *et al.* 2023: Figs 1, 5 & 6); Khaustov and Khaustov, 2023: Fig. 1) or scanning electron microscope (SEM) micrographs (e.g. Khaustov and Khaustov, 2023: Figs 4 & 5; Wergin *et al.*, 2000).

The redescription of any species, however precise it is, must be based on mites of the same provenance as the type series. This might bear serious problems as emphasized above with *Lasiotydaeus*. The species "*Lorryia formosa*" described inadequately as demonstrated above, offers another example. The species was never redescribed from the type series, nor from specimens of the same provenance (citrus in northern Africa). The specimens of *Lorryia* *formosa* described by Jeppson *et al.* (1975, fig. 85) are probably American and bear the same binomen as the African species described by Cooreman (1958). Yet, they differ on several points: the reticulation pattern as well as the length, shape (rounded vs sharp end) and insertion of some setae (P3, L1).

Ontogeny and sexual polymorphism

In the past, genera were erected and based on misidentified immature specimens: the so-called genus *Hypopus* by Dugès (1834: 20) is a famous example. In Tydeidae, a nymph in pupation was illustrated, without understanding what it was, by Berlese (1910: figs 5, 5a): *Tydaeus* (*Tydaeolus*) *atomus* had four trichobothria.

Tydeus munsteri, the species described by Meyer and Ryke (1959: 413), studied by André (1980: 128) and by Ueckermann and Grout (2007: 2062-2064) and designated as the type species of *Afrotydeus*, has 6 genitals and not 4 as noted by Baker (1970: 164) and exhibits the same phanerotaxy as the nominal subgenus *Tydeus*. The confusion between a tritonymph with 4 genitals and the imago with 6 genitals might explain the misunderstanding.

The hypothesis suggested by Ueckermann and Grout—the specimen studied by Baker was a tritonymph—is all the more attractive as the confusion imago-tritonymph was also made by him when he described the holotype of *meyerae* Baker (1970: 165), the type species of *Perafrotydeus*. The holotype was examined by André (1980: 142) who stated that the holotype was not a female but a tritonymph in pupation.

A problem also concerns the genus *Edlorryia* based on a unique specimen of Baker (1968), a deutonymph the chaetotaxy of which was incompletely published.

Additionally, laboratory colonies attested thelytoky in tydeid mites (Hernandes *et al.* 2006; Silva *et al.* 2014) and confirmed the sex ratio observed in the field; it is an open question whether this trend is comparable to those observed in Oribatida (Heethof *et al.* 2009). A last problem concerns the striation pattern which could vary between males and females as shown by Khaustov (2023), such a secondary sexual dimorphism complicates the species identification and recalls the heteromorphic males observed in Iolinidae by Kaźmierski (1998b: 43).

Group of species vs complex of species

As already proposed by Athias-Henriot (1975), the development of identification tools has nothing in common with systematic research, clearly visible morphological traits are sufficient for this approach. Currently, the genus *Brachytydeus* contains 220 species and it is difficult to discriminate them. Grouping tydeid species with similar morphology is an old tradition already used by Koch (1850: 71), Oudemans (1929: 480), Baker (1968: 987) and Kaźmierski (1980: 89) and might help to make accurate identifications.

As noticed by Zachos (2016), species names are discrete units in a continuous world with fuzzy boundaries and species close to one another might be grouped in species complexes as already done in Eriophyidae species associated with particular crop systems (de Lillo *et al.*, 2018). Contrarily to species group where similarity is a key point, phylogenetic criteria are important and might help to detect close or cryptic species, for instance those living in the same agroecosystem such *Brachytydeus formosus* collected on citrus. Such complexes in Tydeidae are evoked by Parker (1982: 123). As demonstrated by Halliday (2010) and Saccagi and Ueckermann (2024), close species may be a source of taxonomic and nomenclatural confusion that potentially complicates pest management and biosecurity.

Unresolved hypotheses

Only unresolved hypotheses related to species of agronomic importance are listed hereafter.

Tydeus californicus (Banks) is suspected to be a junior synonym of *T. spathulatus* by Ueckermann and Grout (2007: 2364). Similarly, Ueckermann *et al.* (2019: 505) are questioning the identity of the Turkish specimens of *Tydeus californicus* (Banks) as the expanded caudal setae (spatulate) differs from specimens from the USA (lanceolate). The true identity of Turkish specimens is again questioned by Akyazı *et al.* (2024: 1039). *Tydeus goetzi* Schruft was first identified as *T. caudatus* by Akyazı *et al.* (2017: 12). *Tydeus caudatus* auctorum might designate *T. goetzi*, at least in some cases (André, 2021: 1031).

Lastly, *Tydeus viburni* Koch has never been recorded since the original description in 1838. However, *viburni* was listed with *Tetranychus urticae* by Pritchard and Baker (1955: 437). *Tydeus viburni* might be the old name of *T. goetzi* since both mites are frequent on *Viburnum* (André, 2011: 77–80). The hypothesis was advanced by André (2021: 1031).

Conclusions

All tydeid genera are now defined by meristic characters (chaetotaxy, solenidiotaxy…) and not based on the ornamentation (striation pattern, reticulation, basketweave…). Some traits are neglected such as the number of opisthosomal setae (9 vs 10) or the epimeral setae. The new nomenclature is simpler than in the past (there were 3 synonymies and 1 homonymy for *Venilia* and 3 chaetotaxies for the same genus, *Afrotydeus*) and accords with ICZN. A type species is fixed for all genera. The number of genera (31) and non-nominal subgenera (3) remains almost the same as in the past, even after the nomenclatural changes above-mentioned.

Any classification—whatever it is—is a taxonomy based on our current knowledge of mites and not a classification **of mites themselves**. Our knowledge is so meager (3.72% of morphospecies, still less if cryptic species are considered) that it allows to explore evolutionary trends of some traits but not to define a real phylogeny of species. Lastly, the classification proposed does not reflect the intra-population variations, nor the variations both within and between species. Species names are discrete units in a continuous world with fuzzy boundaries, *a fortiori* that applies to genus names. Acarology is still in its infancy…

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