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Review Article

Evaluating Alpha and Beta Taxonomy in Ant-Nest Beetles (Coleoptera, Carabidae, Paussini)

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We evaluated completeness, accuracy, and historical trend of the taxonomic knowledge on the myrmecophilous ground beetle tribe Paussini (Coleoptera, Carabidae, Paussinae). Accumulation curves for valid names and synonyms of species, subgenera, and genera were modelled using logistic functions. Analyses of trends in synonymies suggest that few currently accepted taxa will be recognized to be synonymous in the future. This may indicate that Paussini are a taxonomically relatively stable tribe of carabid beetles. However, this result might also be due to the lack of recent taxonomic work in some biogeographical regions.

1. Introduction

Arthropods are the most diversified animal group [1, 2]. Although it is widely acknowledged that only a small fraction of the extant arthropod species has been described, the magnitude of the so-called Linnean shortfall (i.e., the discrepancy between the number of described species and the number of living species) is a matter of discussion [2]. Also for relatively well-investigated arthropod groups, there is few information about the quality of the taxonomic knowledge [3, 4]. The most basic question is to establish how complete and accurate the taxonomic status of a given group is. With the word completeness we refer here to the problem whether the species list of a given group can be considered fairly complete or if there are still many species to describe. A completely known group is one for which there is no longer a need of an alpha taxonomic work (the discovering and naming of new species [5]). With accuracy we refer to taxonomic stability. An accurately known group is one for which there is no more need of a beta taxonomic work (the study of the relationships between the already described taxa, through systematic revisional work of higher taxa [5]). Because it is not rare that species are redundantly described under different names (i.e., synonyms), a group is known with accuracy when no relevant taxonomic change is expected.

Although the two aspects tend to be interrelated, they are not necessarily redundant, because revisional works are much rarer than descriptions of new taxa.

In this paper, we evaluated the completeness and accuracy of the taxonomic knowledge about a group of myrmecophilous beetles, the tribe Paussini ("ant-nest beetles") of the family Carabidae (Coleoptera, Adephaga, Paussinae), at a global level.

All Paussini are highly specialized social parasites, depending on ants (mainly associated with Myrmicinae and Formicinae) during any stage of their development [6–9]. Adults prey on ants and their broods without any obvious benefit for the ant colonies [10–15]. Because of their specialised behavioural and morphological adaptations, Paussini have long attracted the interest of entomologists working on myrmecophilous insects [13], and they have been recently into focus because of strong incertitude about their relationships with other Paussinae lineages [6, 7]. These studies have prompted our knowledge of Paussini biology,

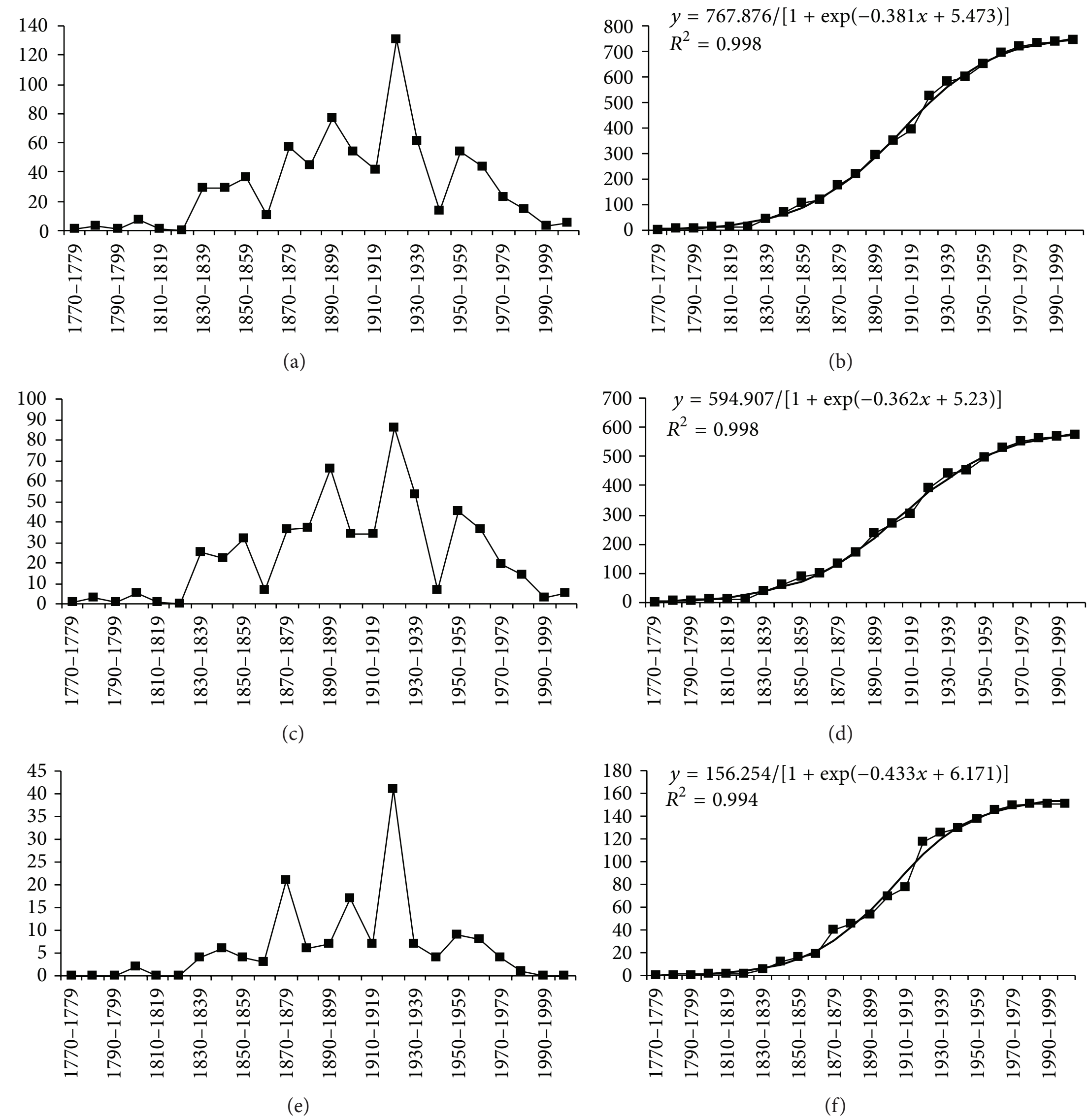

Figure 1: Numbers of total described taxa (a, b), valid species (c, d), and synonyms (e, f) of Paussini by decade. Figures (a), (c), and (e) report the absolute numbers, and Figures (b), (d), and (f) the cumulative numbers along with the equations of the fitted curves.

with emphasis on their immature stages and microscopic morphology, but taxonomical work seems to receive little attention.

In general, for assessing the status of the taxonomical process in a given group, the study should be addressed to describe (1) the growth through time of the cumulative number of valid names to estimate the number of species that remain to be discovered in a given taxonomic group, globally or regionally [4, 16–19], (2) the progression of the cumulative number of invalid names (synonyms), and (3) the temporal trends in the proportion of synonyms [20, 21]. Presence of a plateau is considered evidence that no, or few, species remain to be described, but it can be also due to a stop in taxonomic research [22]. In this paper we present an extension and continuation of a recently published study [22] where we have presented a comprehensive treatment of point 1. In the present paper we will treat the additional aspects of points 2 and 3 taking advantage of the statistical methodologies developed in the former paper.

2. Material and Methods

2.1. Data Collection. We used a computerized database including 572 species and 17 subspecies of the tribe Paussini.

The following information was recorded for each species and subspecies: generic assignment, subgeneric assignment, author, year of description, synonyms, and the biogeographical region of species distribution. We also recorded authorship and year of description of genera (see [22] for details).

2.2. Historical Accumulation Curves of Valid Names and Synonyms. We extracted the year of description of all valid

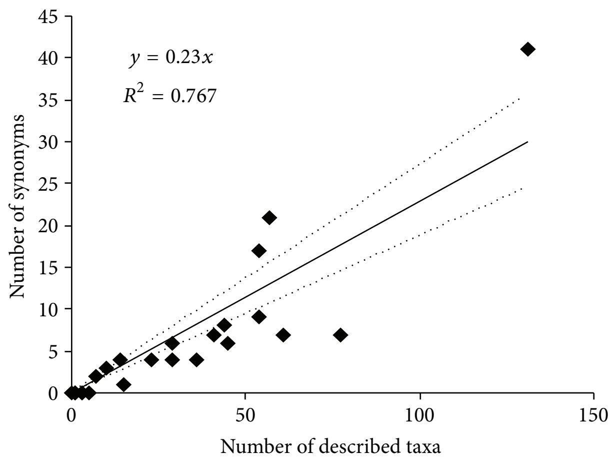

Figure 2: Relationship between number of synonyms and total number of described taxa per decade. Ordinary least square (OLS) regression forced to pass through the origin.

species and subspecies names, as well as the year of description of the names that are currently considered synonyms and grouped years into decades. We plotted the raw number of described taxa, and the raw number of valid taxa, the raw number of synonyms, as well as their cumulative number, against the decade of description.

To model species accumulation curves we used the logistic function $y = b_0/(1 + \exp(b_1 x + b_2))$, where b_0, b_1, and b_2 are estimated parameters, because it gave excellent fits and the first parameter (b_0) is the upper asymptote, thus providing an immediate estimate of the expected number of taxa. Similar analyses were conducted for genera and subgenera. The use of subgenera in the tribe Paussini is very controversial. For this reason, as in our companion study [22], we used subgenera as currently accepted by most authors [23].

2.3. Trends in Synonymies. Both the historical accumulation of species names and the relationship between valid species and synonyms may provide information about the status of the taxonomical knowledge in a given group [24].

Thus, we modelled synonym accumulation curves and measured the temporal variation in the taxonomical efficiency through time in three ways: (1) as the relationship between the number of synonyms versus the number of total described taxa in each decade, (2) as the proportion of names that are now regarded as synonyms over the total number of taxa described in that decade, (3) as the cumulative proportion of synonyms through decades.

Relationship between the number of synonyms versus the number of total described taxa was substantially linear, and we used an ordinary least squares (OLS) regression to model it. We forced the regression to pass through the origin, because when no taxon is described, the number of synonyms must be zero. We used the coefficient of the regression line as a measure of the number of synonyms introduced—on average—for each species in each decade. We used the 95% confidence limits to identify decades with exceptional number of synonyms.

Proportion of synonyms was used as a measure of the relationship between descriptive (alpha) and revisional (beta) taxonomy. We calculated the proportion of synonymous taxa described in each decade to identify a possible temporal trend in synonym proliferation.

The cumulative proportion of synonyms through decades was used as a rough measure of the quality of currently valid names. Following Baselga et al. [24] we assumed that the more taxonomical revisions are carried out, the higher is the probability for a given species name to be synonymized. Given that the synonyms are assigned to the date when the name was introduced, rather than the date when it was recognized as a synonym, the percentage of synonyms will show a diminishing trend with time, as newly described species will have had less time to be reviewed and eventually synonymized [24]. Irrespective of that, the steepness of the decay of this percentage through time can help us to measure the quality of currently valid names.

3. Results

The rate of species description per decade, when the absolute numbers are considered, is very irregular (Figure 1(a)). Between 1775 (when the first species of Paussini was described by Linnaeus) and 1840 only 31 species were described, and no species was described in the decade 1820–1829. In the latter half of the 19th century species were described at an increasing rate, with two peaks, respectively, in the decades 1870–1879 and 1890–1899, in which a total of 38 Paussini taxa were described. However, the description of species peaked between 1920 and 1929, during which period 131 taxa were described, covering almost 17% of the available names. The low level of species descriptions in the decades 1910–1919 and 1940–1949 may be explained by the effects of the First and Second World Wars. Since the 1950s descriptions decreased progressively. When the cumulative numbers are considered, the increase per decade was low until the 1840s. The cumulative numbers of species/subspecies descriptions have reached a plateau, the estimated asymptotic value for the fitted curve being 768 taxa (Figure 1(b)).

Analyses omitting synonyms and subspecies revealed similar patterns (Figure 1(c)), with an estimated asymptotic value of species number at 595 (Figure 1(d)). Because the number of currently recognized valid species is 572, the model predicts the existence of 23 undescribed species, with about 96 per cent of the world fauna described.

Patterns in synonyms were also similar to the general trend (Figures 1(e) and 1(f)). The asymptotic value for the number of synonyms is 156 names, very close to the current number of recognized synonyms.

Number of synonyms per decade was directly proportional to the number of described taxa, with a mean rate of one synonym per four taxa each decade (Figure 2). However, the decades 1870–1879, 1900–1909, and 1920–1929 were characterized by an exceptional high number of synonyms. An in-depth analysis of the percentage of synonyms per

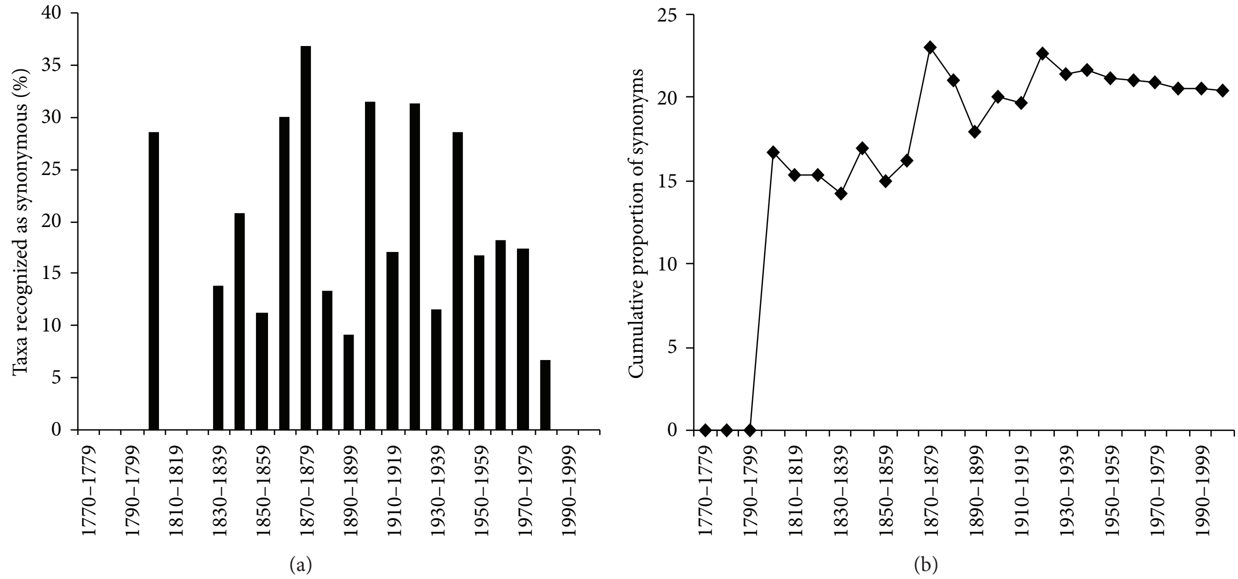

Figure 3: Percentages of synonymous taxa described in each decade (a) and their historical process of accumulation (b).

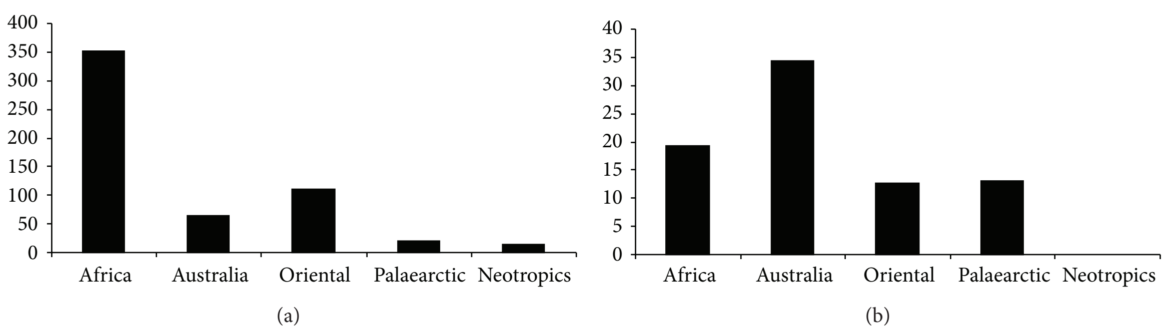

Figure 4: Number of valid species of Paussini per biogeographical region (a) and percentage of synonymous taxa of Paussini per biogeographical region (b).

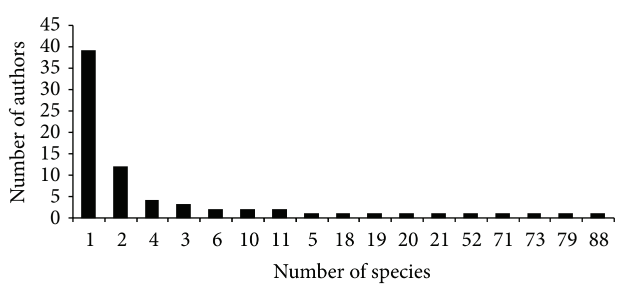

Figure 5: Number of authors in relation to the numbers of species of Paussini that they described.

decade shows a roughly humped trend, with proportion of synonymous taxa increasing from 1830–1849 to 1870–1879, and then decreasing to very low values (Figure 3(a)), which determines a plateau in the accumulation curve of synonymies (Figure 3(b)).

The historical process of variation in proportion of synonymized names defines the following time spans that correspond to periods of roughly homogenous taxonomical work (Figure 3(a)): (1) the very early stage was obviously characterized by few descriptions (cf. Figure 1) which are still valid species; (2) the relative rate of redescriptions was nearly constant between 1800 and 1870; (3) between 1870 and 1930 we found that at increasing description of species there was also an increasing number of species subsequently found to be synonymous; and (4) finally, from 1930 to present time, the relative rate of descriptions subsequently synonymized diminishes drastically, as less than 20% of the species described during this period have been synonymized (Figure 3(b)).

The largest numbers of described species occur in Africa, followed by the Oriental and Australian regions (Figure 4(a)). This pattern is not paralleled by proportion of synonymies, with the Australian fauna being that with the highest percentage of synonymized taxa (Figure 4(b)).

The distribution of the numbers of authors that have described Paussini taxa is strongly right-skewed (Figure 5). Over 52% of authors have described only one species. The most productive author, Reichensperger, described 88

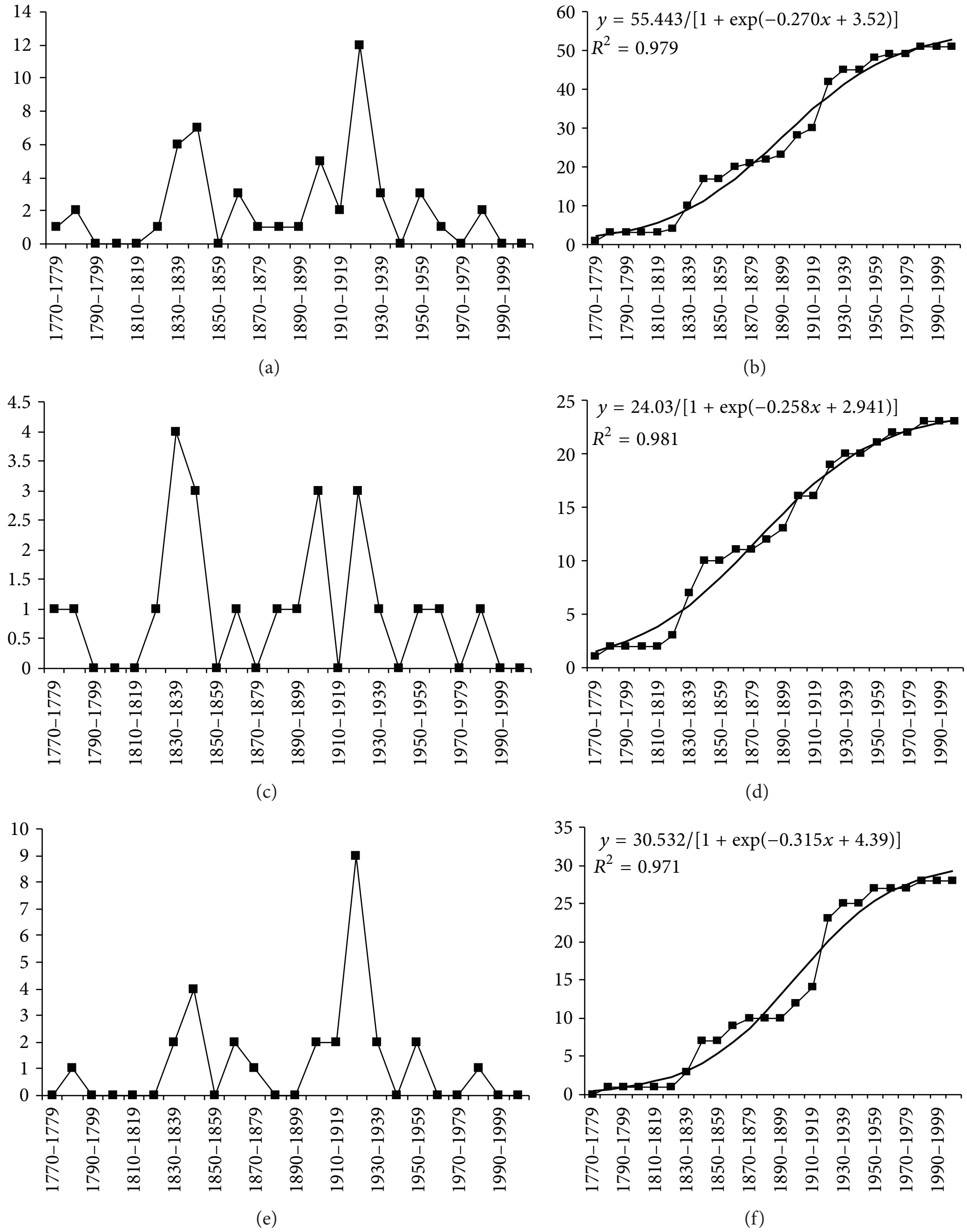

Figure 6: Numbers of total described genera (a, b), valid genera (c, d), and synonyms (e, f) of Paussini by decade. Figures (a), (c), and (e) report the absolute numbers, and Figures (b), (d), and (f) the cumulative numbers along with the equations of the fitted curves.

species, followed by Westwood (79), Wasmann (73), and Luna de Carvalho (71). Altogether, these four authors described more than 40% of known species.

Reichensperger published his descriptions between 1913 and 1958 (with an average of ca. 2 species per year), covering all biogeographical regions except the Australian. Most of his species (ca. 94%) were described from Africa. Westwood made his descriptions between 1833 and 1874 (with an average of more than 6 species per year) covering all biogeographical regions with a high proportion (ca. 41%) of Oriental taxa. Wasmann also covered all biogeographical regions between 1892 and 1930, with similar proportion of African (49%) and Oriental (42%) taxa and a mean rate of ca. 2 species per year. Finally, Luna de Carvalho described most of his species from Africa (ca. 85%), with a few species from the Oriental and the Palaearctic regions.

Paussini species are currently allocated in 23 genera. The total number of described genera is 51, with 28 synonyms

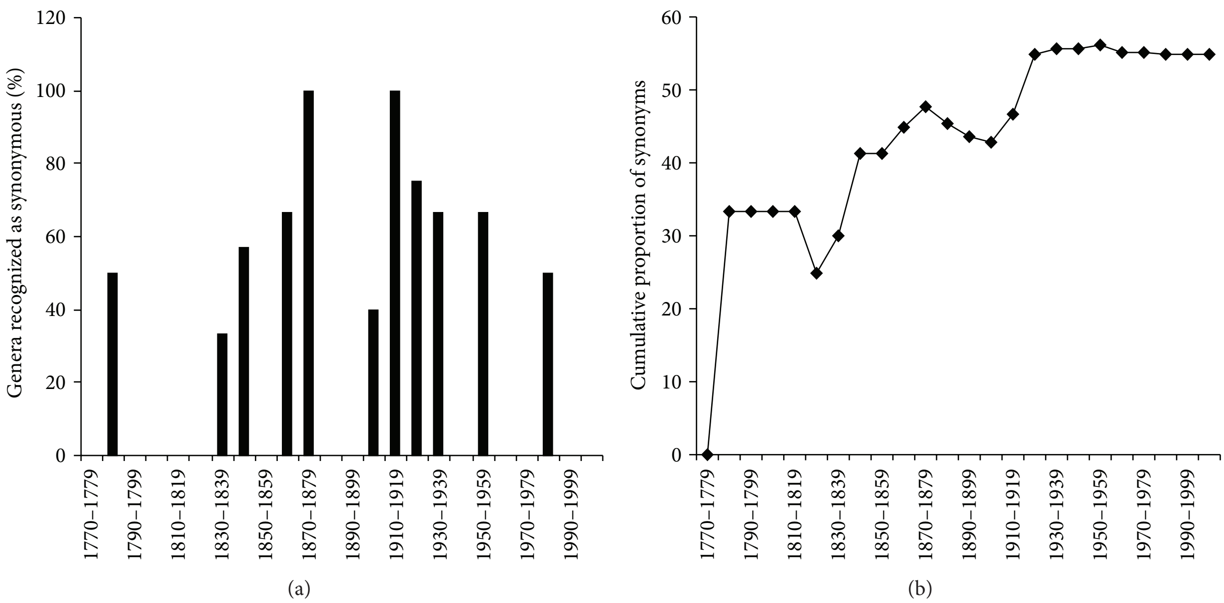

Figure 7: Percentage of synonymous genera described in each decade (a) and their historical process of accumulation (b).

(55%). Most of the genera were described in the decade 1920–1929 (Figure 6(a)). Although some decades were characterized by a high number of descriptions of genera, many were recognized as synonyms (especially among those described in the decade 1920–1929) (Figure 6(e)), so the decade with the highest number of valid genera (4 genera) was 1830–1839 (Figure 6(c)): 75% of the genera described in the decade 1920–1929, and 50% of those described in 1980–1989, were subsequently recognized as synonyms.

Patterns of genera accumulation through time indicate a good sigmoid shape for the total number of species (Figure 6(b)), valid genera (Figure 6(d)), and synonyms (Figure 6(f)). In all cases, a plateau has been reached, so virtually no new genus is expected for the future. The historical process of variation in proportion of synonymized genera indicates that after the 1930s there is a substantial stabilization (Figure 7).

The study of subgenera indicates a proliferation of names in the periods 1920–1929 and 1980–1989 as for the genera (Figure 8). Although these were the two decades which mostly contributed to the current accepted subgenera, these were also the decades in which a large number of synonymous subgenera were described, with proportions of synonyms of more than 54% and 64%, respectively. Accumulation curves showed a stair shape pattern, with apparent plateaus, and were therefore not modelled with fitting curves (Figure 8). Moreover, the historical process of variation in proportion of synonymized genera indicates that there is no substantial stabilization (Figure 9). This was mostly due to the large number of subgenera proposed in a recent time (1980–1989) and subsequently synonymized (Figure 9). These patterns suggest that subdivision into subgenera is not reaching a definitive solution.

Species allocation among genera is strongly dominated by the richest genus (*Paussus*), with 342 ascribed species (Figure 10) and 25 subgenera. Species distribution among subgenera is also very uneven: the subgenus with the highest number of species is *Cochliopaussus* (Figure 11).

4. Discussion

Species accumulation curves of the world Paussini fauna indicate that this tribe of carabid beetle is taxonomically stable but do not prove that knowledge is exhaustive. According to the trends analyzed in the present paper, relatively few species are expected to be described in the future on morphological basis and few currently accepted taxa will be recognized to be synonymous. However, if this situation may reflect a true state of affairs in the best explored regions, it may be an artefact when stabilization is merely due to prolonged taxonomic inactivity.

In general, temporal trends in species descriptions mirror dramatic events in human history. The first peak in African species description occurred in the decade 1880–1899, which can be considered an indirect reflection of the first phase of African explorations that occurred between 1840 and 1870 and especially a direct effect of the German expansion in Africa in the 1880s. The second peak occurred in the decade 1920–1939, which coincides with the third phase of the African colonialism, during which the most influential European states organized and stabilised their territories. The overall trend in species descriptions shows two falls in correspondence with the First and Second World Wars. If taxonomic research was frozen at those dates, we would have a completely false signal of stability. For example, taxonomic

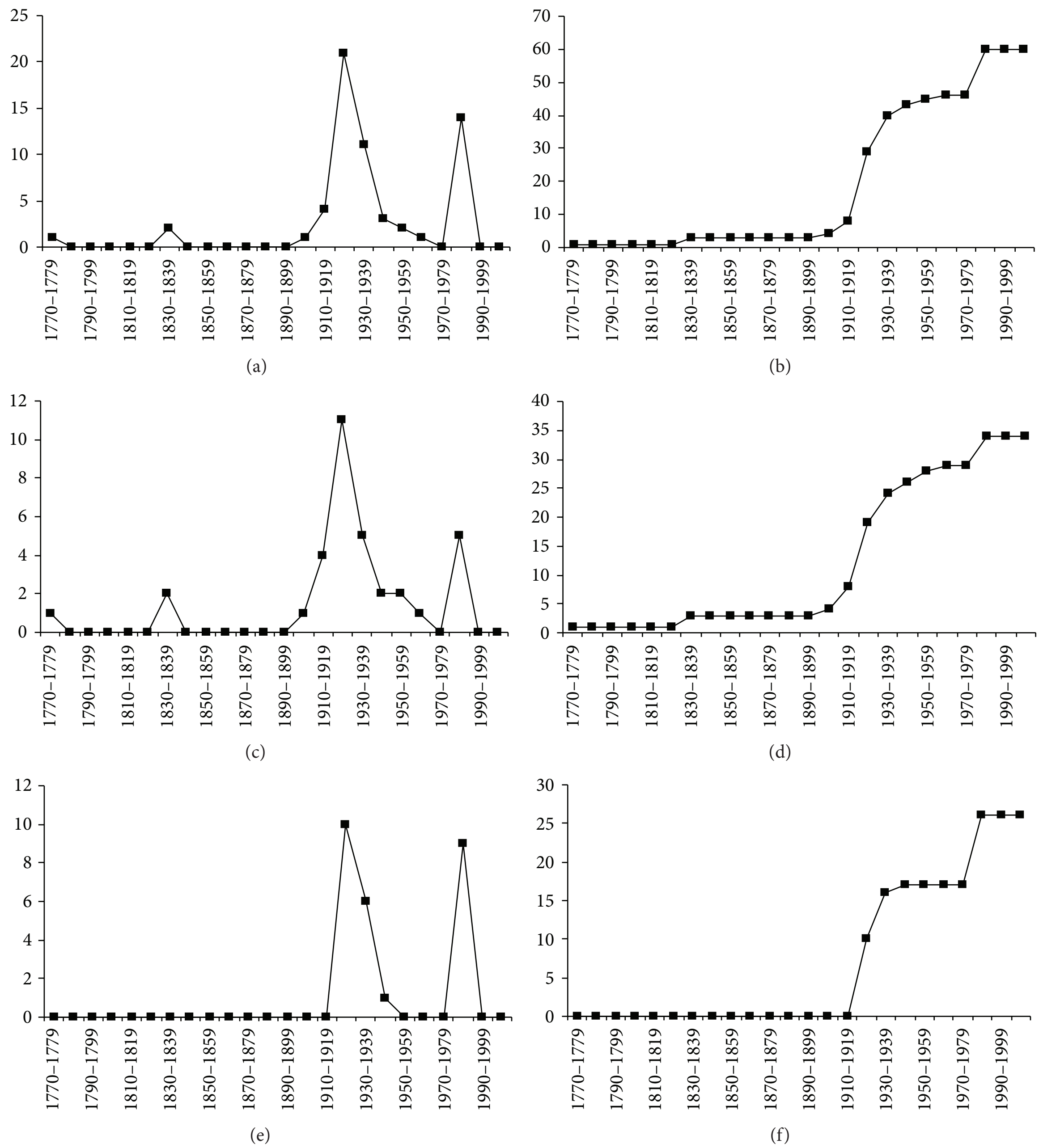

Figure 8: Numbers of total described subgenera (a, b), valid subgenera (c, d), and synonyms (e, f) of Paussini by decades. Figures (a), (c), and (e) report the absolute numbers, and Figures (b), (d), and (f) the cumulative numbers.

knowledge in Australia rested at the 1930s [22]. The lack of recent taxonomic activity, coupled with the low number of described species and the high percentage of synonyms, indicates that the fauna of this region is still poorly known.

Most of taxonomic work on Paussini has been produced by few but very prolific authors. Moreover, the authors that described most species during the 20th century were the same that realised the most comprehensive revisions. This has created a self-referenced system, with an almost complete lack of plurality of views. Therefore, taxonomic stability is largely an effect of the "monopolistic" position of certain taxonomists (e.g., Reichensperger, Westwood, Wasmann, and Luna de Carvalho) for long times. Moreover, each of the most active taxonomists was mostly interested in a different biogeographical region, thus with limited taxonomic overlap.

At global level, the asymptotic value calculated for the synonym curve is very close to the current number of synonyms (151); thus we expect that virtually no taxa will be recognized as synonymous in the next future. This indicates that new species are still being described (alpha taxonomy), albeit at decreasing rate in the best explored regions, whereas virtually no synonyms are currently being

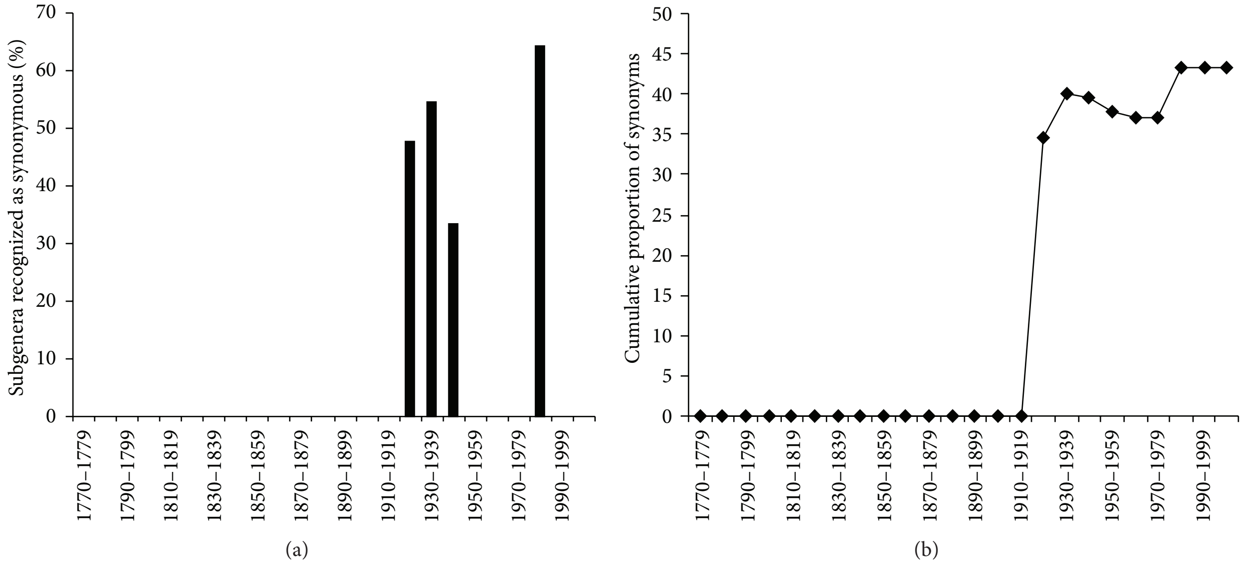

Figure 9: Percentage of synonymous subgenera described in each decade (a) and historical process of accumulation of percentage of synonyms over the total number of names in the Paussini, according to the date of their description (b).

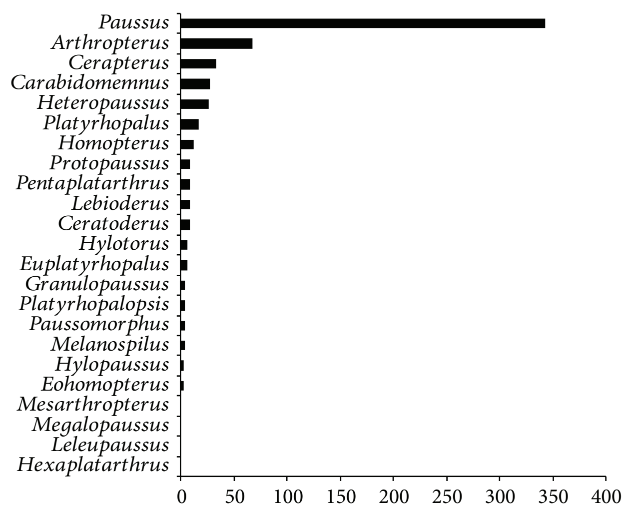

Figure 10: Number of species per genus in the tribe Paussini.

described, implying either a lack of beta taxonomy (i.e., redundant descriptions are still considered valid because of the reduced revisional work) or an excellent efficiency of alpha taxonomy (i.e., all new species are valid and none is redundantly described) [24]. We think that failure to recognize synonymies is likely high in the less studied faunas, for which most species have been described from sparse individuals, but this is balanced by the presence of still undescribed species. This may be the case of the Oriental region, which seems to have few species and a moderate percentage of synonymies, but from which so many species are being discovered and no further synonymies established.

Stability in species beta taxonomy indicates that Paussini species are recognized as discrete entities by most researchers. Paussini species were described and are currently recognized on the basis of morphological traits, that is, as groups of phenetically similar individuals that can be separated from other analogous groups by means of phenetic gaps, thus corresponding to a morphological concept of species [25]. Stabilization in synonymies suggests that most taxonomists agree in considering the diagnostic characters presented in species descriptions as gaps sufficiently strong to mark discontinuities among populations. Morphologically defined species do not necessarily correspond to "biological" species (defined as reproductively isolated populations [5]). However, the application of a morphological approach for discriminating species was the practical methodology most frequently used by taxonomists in the past, and the same approach still dominates (and likely will dominate) daily work of the majority of taxonomists. Stability in beta taxonomy of

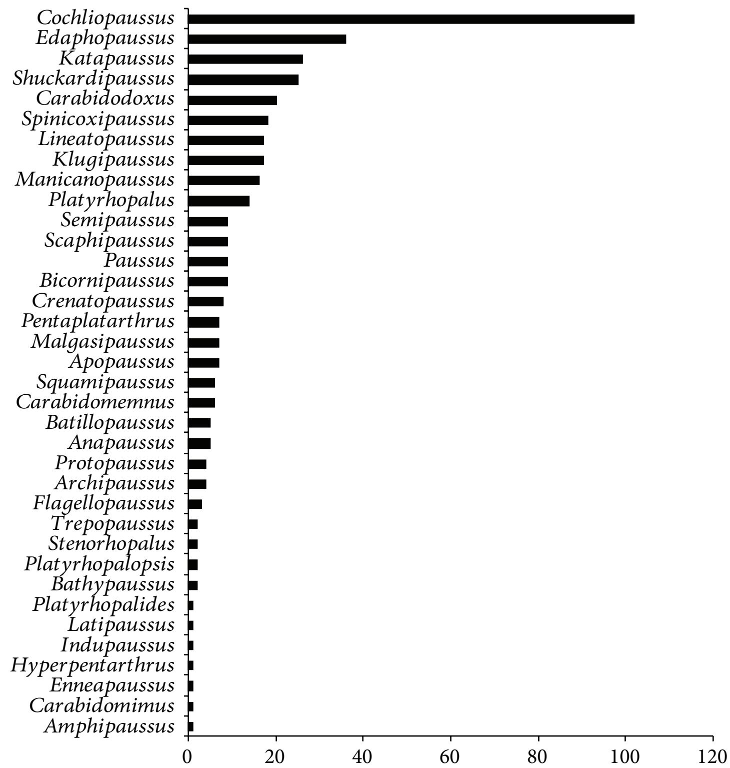

Figure 11: Number of species per subgenus in the tribe Paussini.

morphological species makes Paussini an ideal candidate for future works using molecular approach to investigate how morphological discontinuities are paralleled by molecular divergences. This would be particularly important to clarify relationships among species. Current taxonomic patterns suggest that most species were allocated into the genus *Paussus* probably reflecting a real phylogenetic proximity. However, subgeneric divisions appear instable and based on subtle and controversial morphological characters. This suggests that morphological characters are not fully adequate to resolve infrageneric relationships.

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