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Original Article

Species living in harsh environments have low clade rank and are localized on former Laurasian continents: a case study of *Willemia* (Collembola)

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ABSTRACT

Aim Certain species have few living relatives, i.e., occupy low clade ranks. Hence, they possess high conservation value and scientific interest as unique representatives of ancient lineages. However, we do not know whether particular environments favour the maintenance of low clade ranks or whether the distribution of environments across the globe affects the global distribution of clade ranks and, hence evolutionary uniqueness. In this study, we tested whether and how harsh environments decrease the clade ranks of the species that inhabit them.

Location Global

Methods We described the phylogeny of the collembolan genus *Willemia* by a parsimonious method based on 52 morphological characters and estimated the species' use of harsh environments (polar, high-mountain, desert, polluted, waterlogged, saline, and acidic) from 248 publications.

Results We found that the use of different types of harsh environments is maintained among close relatives and has similar phylogenetic signals (except for the use of salinity). The use of harsh environments might therefore affect the diversification of lineages. Correcting for the phylogenetic non-independence of species, we found that species using harsh environments have comparatively low clade ranks. We also found that species using harsh environments occur almost exclusively on former Laurasian continents and that as a statistical consequence, Laurasian species tend to have lower clade ranks.

Main Conclusions We suggest that harsh environments maintain low-clade-rank species by decreasing, simultaneously or successively, extinction and speciation, which may eventually explain the major variation in clade rank across the globe.

54 **Keywords** abiotic stress; diversification; habitat; niche conservatism; phylogenetic
55 reconstruction; phylogenetic generalised least squares; phylogenetic principal components;
56 phylogenetic permutation; root-skewness test; tropical

57

INTRODUCTION

Extant species can occupy very different clade ranks within a phylogenetic topology. Certain species have very few living relatives and thus occupy a low clade rank, whereas others have much higher clade ranks. Species of low clade rank are the sole extant representatives of their lineages and hence have a high evolutionary uniqueness: the loss of a low-clade-rank species implies the loss of more evolutionary history than the loss of a high-clade-rank species (Purvis *et al.*, 2000; Prinzing *et al.*, 2004; Colles *et al.*, 2009). For this reason, it is important to understand whether low-clade-rank species are maintained to a greater extent in certain environments or regions than in others.

It has been suggested that species of low clade rank persist and accumulate in regions with low extinction rates (Willis, 1922; Condamine *et al.*, 2012), notably due to relatively stable climates, especially in the tropics (Wiens & Donoghue, 2004; Jablonski *et al.*, 2006; Hawkins *et al.*, 2007; Donoghue, 2008; Buckley *et al.*, 2010). Furthermore, low clade rank has been suggested to reflect a relatively low speciation rate, as has been proposed for the regions outside the tropics (Willis, 1922; Jablonski, 1993, 1999; Chown & Gaston, 2000; Jablonski *et al.*, 2006). Overall, species of low clade rank can be expected to most likely accumulate in regions in which a low speciation (or immigration) rate very roughly outweighs a low rate of extinction (or emigration). There would be no net effect on species richness under such circumstances.

The distribution of clade ranks across regions has received considerable attention, whereas the distribution of clade ranks across types of environments (broadly, “habitats”) has received much less attention. Bartish *et al.* (2010) have recently shown that within a region, particular harsh environments might be colonised by species of particularly low clade rank: across 40 different habitats in the Netherlands, those with extremely high soil moisture and

extremely low soil pH were characterised by low mean clade ranks of their angiosperm inhabitants. However, this analysis was restricted to a single, small region and might not reflect (or influence) globally coherent patterns. Here, we define abiotically harsh environments as environments that tend to impose a major direct physiological stress on most species of a given lineage — i.e., a constraint on growth and reproduction (sensu Grime, 1977) — with the obvious exceptions of highly tolerant species and sub-lineages. We can speculate that harsh environments might indeed reduce extinction rates, as patches of harsh environments remain present at least locally at any given time in any region and maintain gene flow (Behrensmeyer et al. 1992), and species in harsh environments might rarely be driven to extinction by biotic interactions (Grime 1977, Callaway et al. 2002). In addition, harsh environments might possibly reduce speciation rates by reducing two of the major triggers of speciation: (i) recombination events, which become rarer with environmental harshness due to increased generation times (Grime 1977), and (ii) evolutionary arms races between prey and their natural enemies, which become less diverse with harshness due to a reduction in the number of trophic levels (Vermeij 1987). We therefore hypothesise that clade ranks are lower in harsh environments (whereas species richness is not affected).

Whatever the relationship between environmental harshness and clade rank, the existence of such a relationship requires that there is no trade-off between the capacity to use different types of harsh habitats; otherwise, the average harshness of the habitat used by any species would be intermediate (see Hoffmann & Parsons, 1997 for possible mechanisms). The existence of a relationship between harshness and clade rank would also require that the use of harsh and mesic environments is phylogenetically conserved so that related species tend to have similar affinities to harsh and mesic environments (see Prinzing *et al.*, 2001, phylogenetic signal sensu Losos, 2008). Without such conservatism, past patterns of speciation and extinction in ancestral environments would not be transmitted to distributions

of clade ranks in present-day environments (Condamine *et al.*, 2012). However, certain authors suggest that the capacity to use harsh environments can evolve and disappear rapidly (see Hoffmann & Parsons, 1997 and Hoffmann & Willi, 2008 for mechanisms), particularly if expansions and constrictions of such harsh environments may trigger the acquisition or loss of the capacity to use these environments (Gaston, 1998) and if the use of harsh environments imposes a cost (but see Gaston, 2003). We hence hypothesise that the use of harsh habitats is not constrained by a trade-off between different types of harshness and is phylogenetically conserved.

Should particular environments maintain low-clade-rank species and particular regions maintain these particular environments and their inhabitants, we would expect to observe that these regions also maintain many low-clade-rank species (see also Donoghue, 2008). We can speculate that selection might have favoured the use of harsh habitats far from the tropics (Jablonski, 2008), especially in the Northern Hemisphere, where a steep latitudinal gradient of decreasing biodiversity can be observed today (Chown *et al.*, 2004). Given that the clade rank of a species reflects the outcome of millions of years of evolutionary history, the past differentiation of regions, notably the distinction between Laurasia and Gondwana, might be more important than their present-day configuration. One might speculate that past environments were harsher, on average, in Laurasia than in Gondwana (Vršanský, 2005; Crisp *et al.*, 2010), reflecting, among other differences, the larger surface area of the landmasses in northern compared to southern temperate regions. Larger landmass would produce more climatic and thereby edaphic extremes in Laurasia and its descendent land masses than in Gondwana, except for Antarctica (Chown *et al.*, 2004). Additionally, even restricted periods of harsh conditions might leave a strong signal in a continental fauna if the vast majority of the continent became harsh and later recolonisation was slow. This regional origin and maintenance of species might still be reflected by a larger number of low-clade-rank species

in landmasses stemming from Laurasia (centres of origin, Myers & Giller, 1988). Moreover, independent of the above speculations, given what we know of the present worldwide distribution of soils (FAO-UNESCO, 2007), climates (World Climate Map, 2012) and human activities, harsh environments (e.g., soil acidity, drought, frost, waterlogging, heavy metal contamination), with the exception of seashore salinity, appear to be more widely distributed in ex-Laurasian than in ex-Gondwanan continents. Whatever the precise causes, we can hypothesise that non-tropical regions and those of Laurasian origin harbour more low-clade-rank species, largely as a consequence of the increased numbers of species using harsh habitats.

The predictions derived from these hypotheses can be tested across extant species belonging to monophyletic lineages that are ancient (having survived several ecological crises and dating back to the Laurasia/Gondwana epochs), highly diversified and distributed worldwide. Collembola (springtails) are one such old, diversified lineage dating back to the Early Devonian (Hirst & Maulik, 1926; Greenslade & Whalley, 1986; Grimaldi, 2010), and most actual forms, at the family or even genus level, are known from the Cretaceous (Christiansen & Pyke, 2002a, b). Among the cladistic studies conducted on Collembola, the genus *Willemia* deserves special attention given its wide distribution from both an ecological and a biogeographical point of view. The genus is monophyletic and comprises a large number of species for which phylogenetic trees can be reconstructed unambiguously (D’Haese & Weiner, 1998; D’Haese, 1998, 2000 for subtrees of the genus). In addition, certain species of *Willemia* are known for their preferential use of arid (Thibaud & Massoud, 1988), polar (Sørensen *et al.*, 2006), mountainous (Loranger *et al.*, 2001), acidic (Ponge, 1993), saline (D’Haese, 2000), or polluted (Filser & Hölscher, 1997) environments. The genus is also representative of many others in the absence of a time-calibrated phylogeny due to the scarcity of fossil records. This lack of information renders approaches based on branch

length inapplicable but does not affect approaches based on clade ranks. Obviously, *Willemia* is only one out of an almost infinite number of genera. However, studying one genus may help to develop a methodological approach for teasing apart the associations between the use of harsh environments and patterns of diversification within a phylogenetic context. This approach may then be applicable to other genera and larger taxonomic units.

To evaluate the relationship between the use of harsh environments and clade rank, we tested whether (i) the use of different types of harsh environment is positively rather than negatively correlated (i.e., species tend to be able to tolerate either a broad range of harsh environments or none) and is phylogenetically conserved in the sense of being more similar among phylogenetically closely related species than among more distantly related species; and (ii) species using harsh habitats consistently occupy low clade ranks rather than being randomly scattered across the phylogeny, and these harsh environments tend to be the ancestral environments of such low-clade-rank species, which are as numerous as species absent from such harsh environments. To evaluate the relationship between geographic region, use of harsh environments and clade rank, we tested whether species outside the tropics occupy lower clade ranks than species within the tropics, due to a tendency of non-tropical species to use harsher habitats. We also tested whether species on former Laurasian land masses occupy lower clade ranks than species on former Gondwanan land masses, due to a tendency to use harsher habitats. In all analyses we accounted for the statistical non-independence of species. We also conducted character mapping to reconstruct ancestral stages and explore whether the environments and regions used by species are indeed ancestral to the respective (sub)lineage and hence might have influenced the clade rank of the respective species in that (sub)lineage.

MATERIALS AND METHODS

The genus *Willemia* and the reconstruction of its phylogeny

Within the Class Collembola, the genus *Willemia* belongs to the Hypogastruridae family. It differs from other hypogastrurid genera by the total lack of pigment or furcula and the small size of the slender body, which never exceeds 1 mm in length (Thibaud, 2004). According to their life form, all *Willemia* species belong to the euedaphobiont sub-category Bc3b (small size, slender body, no furcula) of Rusek (2007). The study addresses 42 of the 43 species currently known worldwide in this genus (list in Appendix S1b). The absent species was only described in 2011 by D’Haese & Thibaud, so its environmental or geographic distribution is still very far from being sufficiently documented. The genus is distributed worldwide, with 15 species recorded only in the tropics, 25 species outside the tropics and only 2 species present both in the tropics and elsewhere (details about the biogeographic distribution of species in Appendix S2e). A total of 13 species were recorded from continents and islands of Gondwanan origin vs. 20 of Laurasian origin and 9 of uncertain origin (Appendix S2e). As for most Collembola, dispersal modes are still unknown, although sea currents have been suspected to favour long-distance transport (Thibaud, 2007). *Willemia* species live in the soil (from litter to mineral soil, whether acid or alkaline), in psammic environments (beaches, sand dunes, deserts) and in caves, but not all of them are found in harsh environments (Table 1). Overall, the great variation in the biogeographic and ecological distributions of species, together with a sufficient but still-manageable number of species, makes this genus a good model for testing hypotheses about relationships between biogeography, ecology and the evolution of extant species.

The reconstruction of the phylogeny of the genus *Willemia* is explained in Appendix S1a-d. This reconstruction confirmed the monophyly of the genus already established by

D’Haese (2000). We were constrained to use morphological characters, as explained and justified in Appendix S1a. Obviously, speciation may not always leave morphological traces, and such “cryptic” speciation is overlooked if morphological characters alone are considered. This outcome is especially probable in lineages with morphological characters that are few in number or unstable in terms of shape and/or position (among Collembola, e.g., genera *Folsomia* and *Parisotoma*). *Willemia*, however, has numerous characteristics (e.g., hairs, sensilla, vesicles) of stable shape and position. Due to this feature of the genus, speciation is unlikely to be cryptic in *Willemia*. Cryptic speciation may be more frequent at the population level, but such ephemeral population phenomena were not of interest in our study. We also note that a dated phylogeny is not feasible for *Willemia* given the lack of dating points caused by the absence of fossils for this genus.

All analyses were run on each of the 6 most parsimonious phylogenetic trees as well as on a strict-consensus of 6 phylogenetic trees (detailed in Appendix S1: Phylogenetic reconstruction). The results from analyses run on the strict consensus tree are given in the Results section, those from the 6 individual trees in the corresponding appendices (detailed in Appendix S3: Reconstruction of ancestral states)

Use of harsh environments and the biogeographic distribution of *Willemia* species

The use of harsh environments (as defined in the Introduction) was indicated by the occurrence of *Willemia* species in environments known for at least one factor that is thought to be a major constraint for most soil-dwelling organisms (see Hopkin, 1997 for springtails): i.e., xeric, hydric, arctic, alpine, acidic, metallic or saline soils. See Appendix S2a for detailed definitions of these factors and literature research methods and Appendix S2b for references. A ‘harshness breadth’ index was estimated for every species based on the number of harsh

environments in which the species was recorded, scaled from 0 (no harsh environments recorded for the species) to 7 (all harsh environments recorded).

Biogeographic distributions were categorised as (i) tropical (between the tropic latitudes, Inter-Tropical Convergence Zone, ITCZ) or non-tropical (north or south of the tropic latitudes) and as (ii) Gondwanan or Laurasian following the maps by Christiansen & Bellinger (1995), as detailed in Appendix S2e. Appendix S2e also outlines the relationships between tropical/non-tropical and Laurasia/Gondwana classifications and between regions and harshness.

Statistical Analyses

The correlation among uses of different types of harsh environments across lineages was analysed by a phylogenetic Principal components analysis (pPCA), a multivariate method recently devised by Jombart *et al.* (2010b) by extending a methodology developed in spatial ecology and spatial genetics to the analysis of phylogenetic structures in biological features of taxa.

Phylogenetic conservatism is the tendency of closely related species to share similar values for a given trait (typically more similar than distantly related species, Wiens *et al.*, 2010). We predicted phylogenetic conservation of the use of harsh environments, i.e., that related species tend to have similar harshness breadth index values. Here, harshness breadth varied from 0 to 7 harsh environments as defined above. Phylogenetic conservatism for harshness breadth was tested with the Pavoine *et al.* (2010) approach. Briefly, the total trait diversity of the lineage was decomposed across the nodes of a phylogenetic tree by attributing to each node a value measuring the differences among lineages descending from that node weighted by the proportion of species descending from it. Permutation tests (999 replicates)

allowed the attribution of a probability to the observed value. Our principal test was the root-skewness test, which verifies whether phylogenetic distances between species correspond to distances in a given trait. Supplementary tests in Pavoine *et al.* (2010) explore whether trait variation is concentrated on a single node or on a few nodes, but that work cannot be presented in detail here (usually, the former were not significant, whereas the latter were). Phylogenetic distances were measured as nodal distances, i.e., the number of nodes on the shortest path that connects two species on the phylogenetic tree. For measuring distances between species in terms of habitat harshness (a multi-choice variable), we used the simple matching coefficient (Sokal & Michener, 1958): $(a+b)/(a+b+c+d)$, where ‘a’ is the number of harshness types in common, ‘b’ is the number of harshness types with which neither of the species are associated, and ‘c’ and ‘d’ are the numbers of harshness types unique to each of the two species.

Losos (2008) has suggested that the term ‘phylogenetic conservatism’ should only be used if trait change along the phylogeny is slower than Brownian motion and that the term ‘phylogenetic signal’ should be used for the wider phenomenon of correlations between trait distance and phylogenetic distance. However, properly identifying the rate of trait change would require a dated phylogeny, which is not feasible for Collembola. Moreover, whereas change in the use of harsh environments may be considered ‘random’ and not ‘conservative’ from the point of view of phylogenetic reconstruction, it is still much more ‘conservative’ than the changes in the harshness of the environment surrounding the animals. For simplicity, we therefore retain the term ‘conservatism’ and use it in the sense of a pattern, not of a process (see Wiens *et al.*, 2010 for further discussion on phylogenetic conservatism).

We then tested the link between harshness breadth as a response variable and (i) phylogenetic clade rank, (ii) tropical/non-tropical classification and (iii) Gondwana/Laurasia classification as explanatory variables. Any test of hypotheses on the environmental and

geographic correlates of clade ranks of species is vulnerable to the phylogenetic non-independence of species. A classical approach to the problem of phylogenetic non-independence is the use of sister-clade comparisons (Felsenstein, 1985), but this approach is not applicable in our case because sister clades have the same clade ranks by definition. An alternative and more general approach is to include co-matrices of phylogenetic proximity in a phylogenetic generalised least square fit (PGLS) as described in Martins & Hansen (1997), using the method of Grafen (1989) to estimate branch lengths. To increase the symmetry of the harshness breadth distribution, this variable was square-root transformed.

We tested the relationships between the phylogenetic clade ranks of species as the dependent variable and either the species' tropical/non-tropical classification or their Gondwana/Laurasia classification as the independent variable. We conducted alternative analyses, either incorporating the uses of harsh habitats as covariables or not incorporating these uses. As the dependent variable was directly inferred from the species' phylogenetic position and was, thus, a characteristic of the phylogeny, we incorporated phylogenetic non-independence in the explanatory variables as follows. We computed the F-statistic associated with each variable using an ordinary linear model. We then estimated a theoretical distribution of this statistic via the method of phylogenetic permutation described by Lapointe & Garland (2001, see also Harmon & Glor, 2010): closely related species are more likely to exchange values than more distantly related species. The values of the explanatory variables were permuted (999 times) by this approach, keeping the phylogenetic clade rank unchanged. The P-value was then calculated as the proportion of theoretical values of the F-statistic that were higher than or equal to the observed value. We note that species that occurred in both the Laurasia and Gondwana biogeographic domains (6 species) or were on continents or islands of uncertain origin (3 species) and species that were recorded both within and outside the tropics (2 species) were discarded from geographic analyses.

All these methods were implemented in R (R Development Core Team, 2010), which was used for all statistical calculations. The packages used were ade4 (Dray & Dufour, 2007), adephylo (Jombart *et al.*, 2010a), ape (Paradis *et al.*, 2004), and nlme (Pinheiro *et al.*, 2010). The R codes are available upon request.

For character mapping, we used Mesquite (Maddison & Maddison, 2011); specifically, we used parsimony and stochastic character mapping. As both approaches produced the same results, we only present the parsimony mapping, which suffers less from the absence of biogeographic classifications for individual species.

RESULTS

The characters and phylogeny of *Willemia* are provided in Appendix S1b and Appendix S1d, respectively. Note that there is no phylogenetic structure in the study intensity of *Willemia* species (i.e., the numbers of references), and hence, the analyses presented below are not biased by study intensity (Appendix S2c). Although branch lengths are not available, as explained in the Introduction, there is a major variation in the clade rank of species, ranging from 2 to 13, reflecting substantial variation in the number of extant close relatives across species.

Uses of most types of harsh habitats are positively correlated

The phylogenetic principal components analysis (pPCA) indicated strong positive correlations between all types of harsh habitats with the exception of salinity. The use of all other types of harsh habitats showed clear positive scores on the same principal component axis (Fig. 1). A visual examination of Table 1 (where species are arranged according to their order in the phylogenetic tree) confirms this result: with the exception of salinity, the use of all types of harsh habitats appears to be phylogenetically positively correlated. Given that the use of saline habitats corresponded to the absence of all of the other six types of harsh habitats, we excluded salinity from further analyses to better capture the overall syndrome of harsh habitat use (see also Appendix S2d).

Phylogenetic conservatism in the use of harsh habitats

The types of harshness under which species were found exhibited clear phylogenetic conservatism (root-skewness test $P=0.002$). Additionally, the number of types of harsh

habitats used by a species (harshness breadth) was phylogenetically conserved (root-skewness test; $P=0.042$). If salinity was excluded from the array of harsh habitats (given that it is not positively related to other harshness factors, see above), a stronger conservatism of harshness breadth was found (root-skewness test $P=0.013$). The presence/absence of *Willemia* species in harsh habitats (rather than the number of harsh habitats used) exhibited an even clearer phylogenetic conservatism if salinity was excluded from the array of harsh habitats (root-skewness test $P=0.001$). This phylogenetic structure was confirmed using parsimony character state reconstruction (Fig. 2 a). These results are based on the consensus tree but are robust to phylogenetic uncertainty and were found in all 6 of the equally parsimonious trees (Appendix S3).

Species using harsh habitats have lower clade ranks but are as numerous as species using mesic habitats

We found that the clade rank of a species decreased with the species' harshness breadth (PGLS; $P=0.002$). If salinity was excluded, it appeared that the distance to the root of the phylogenetic tree was quite similar for all species using harsh habitats independently of the number of harsh habitat types they were using, with all harshness-tolerant species occupying a basal position (Fig. 3). The ancestral nature of life in harsh habitats was also visually assessed through parsimony character state reconstruction (Fig. 1 a), mapping the use of harsh habitats (salinity excluded) and other habitats on the cladogram. Most of the 22 harshness-tolerant species were located close to the root, i.e., they corresponded to a "basal" pool of species including all species from *W. multilobata* to *W. denisi* in Fig. 1 a. Only three species in this group did not confirm that harshness tolerance was an ancestral character: *W. bellingeri*, *W. psammophila* and *W. unispina*. Species belonging to the most advanced group, in contrast,

were not found in harsh habitats (except for saline habitats) with the exception of *W. nepalensis*. All these results are based on the consensus tree but are robust to phylogenetic uncertainty and were found in all 6 of the equally parsimonious trees (Appendix S3).

In total, there were 22 species using harsh habitats and 20 species using only mesic habitats (i.e., species that were never recorded in any of the harsh habitat types considered except salinity). This result is not significantly different from equality ($df=1$; $\chi^2=0.095$; $P=0.758$).

Geographical distribution: species using harsh habitats tend to be Laurasian, and as a statistical consequence, Laurasians tend to have low clade ranks

We found that species using harsh and mesic habitats were distributed differently across the globe. Species using harsh habitats tended to occur in non-tropical regions, although the relationship was relatively weak (Fig. 4a; PGLS; $df=30$; $t=2.29$; $P=0.029$). At the same time, species using harsh habitats were strongly restricted to regions of Laurasian origin (Fig. 4b; PGLS; $df=30$; $t=3.19$; $P=0.003$). In fact, only two harshness-tolerant species were recorded outside former Laurasia (*W. trilobata* and *W. namibiae*, Appendix S2e). These results are based on the consensus tree but are robust to phylogenetic uncertainty and were found in all 6 of the equally parsimonious trees (Appendix S3).

Low-clade-rank species were strongly restricted to present non-tropical regions (Fig. 5a; $n=31$ as in all tests of this paragraph, tests based on phylogenetic permutations, $F=26.14$; $P=0.001$, and see character state reconstruction, Fig. 1b). This relationship was maintained if harshness breadth was included as a co-variable: harshness breadth and presence in present-day non-tropical regions were both related to low clade rank ($F=23.90$; $P=0.001$ for harshness breadth, and $F=9.76$; $P=0.007$ for presence in present-day non-tropical regions; conclusions

were not impacted by the order in which the two explanatory variables were entered in the model; harshness first: $F=29.17$; $P=0.001$, harshness second: $F=4.48$; $P=0.048$). Therefore, the high harshness tolerance of non-tropical species did not explain their low clade rank. Species of low clade rank also tended to be restricted to former Laurasia regions (Fig. 5b; $F=10.47$; $P=0.006$ and see character state reconstruction, Fig. 1c). If occurrence in former Laurasia was included first in the model and harshness breadth second, both variables were significant ($F=12.68$; $P=0.002$ for occurrence in former Laurasia and $F=7.33$; $P=0.014$ for harshness breadth). However, this relationship disappeared if harshness breadth was added to the model first: in this case, occurrence in former Laurasia was no longer significant ($F=1.31$; $P=0.262$), whereas harshness breadth was still significantly related to low clade rank ($F=18.69$; $P=0.001$). Overall, this result indicates that species using harsh environments are particularly bound to former Laurasia continents (above paragraph) and that — as a statistical consequence — we find many species of low clade rank on former Laurasia continents. All these results are based on the consensus tree but are robust to phylogenetic uncertainty and were found in all 6 of the equally parsimonious trees (Appendix S3).

DISCUSSION

We found that uses of different types of harsh environments are maintained among close relatives and have similar phylogenetic signals with the exception of use of saline habitats. Use of saline habitats is thus not consistent with our hypotheses (see Introduction) and was excluded from further analyses. There are two opposing lines of explanation for this exception. First, one can argue that tolerance of saline conditions comes with a major cost in terms of tolerance of multiple other harshness factors, and thus, salinity tolerance will not increase the overall capacity to use harsh environments and will be lost rapidly through

evolution if no longer needed. Second, there are putative arguments suggesting that salinity is not a form of harshness from the point of view of Collembola (Appendix S2d). Pending more ecophysiological studies on the tolerance of springtails to sea water, it might be suggested that life in contact with dilute saline solutions (seashores but not dry saline environments) requires no special adaptation in basal Hexapoda, in contrast to fully terrestrial insects (higher insects).

Using a phylogenetic framework, we showed that among *Willemia* springtail species, the use of harsh habitats (tolerance of harshness) displayed a strong pattern of phylogenetic conservatism and no phylogenetic trade-off in the capacity to use different types of harsh habitat (except for salinity, see Appendix S2d). These results ultimately suggest that the use of harsh habitats can affect the mode of diversification of these lineages and, thereby, the distribution of clade ranks across habitats and eventually regions. In fact, we found that species using harsh habitats have significantly lower clade ranks.

Although the occurrence of archaic life forms has already been documented in specific exotic and harsh habitats such as volcanoes, hot springs, deserts and ice caps (Oliver *et al.*, 2000; Nriagu, 2003; Labandeira, 2005; Oliver *et al.*, 2005; Ehrhardt *et al.*, 2007), a systematic link between species clade rank and habitat harshness has not, to our knowledge, been demonstrated previously. Lower clade ranks would be consistent with lower speciation rates in harsh habitats. However, we also found that species using harsh habitats are even slightly more numerous than species using mesic habitats. This combination of results is consistent with a scenario of decreased net extinction of species combined with decreased net speciation in harsh habitats. We stress, however, that we can only speculate on speciation and extinction averaged across time; we do not know whether this pattern reflects permanently low speciation rates combined with permanently low extinction rates or, for instance, initially high speciation and very low extinction rates combined with later very low speciation rates combined with high extinction rates. Both scenarios may produce the same low clade ranks of

extant species. Independently of the precise mechanisms, harsh habitats function today as museums of low-clade-rank species, i.e., of species that are the last extant representatives of ancient lineages.

Such a pattern of conservatism and of the preferential presence of low-clade-rank species in harsh habitats may ultimately result in the global distribution of harsh-habitat species driving the global distribution of low-clade-rank species, as predicted. In fact, we found that species using harsh habitats exhibit distinct geographic distributions — they are more numerous outside the tropics and, in particular, on former Laurasia — and that species of low clade rank match these distributions. In addition, for Laurasia, the occurrence of low-clade-rank species is, in fact, explained by the occurrence of species in harsh habitats. For this reason, the geographically conserved use of harsh habitats decreases the phylogenetic clade rank of species on the continents of former Laurasia.

Our results contribute to the debate on the evolutionary fate of ‘generalists’ versus ‘specialists’. Generalists are thought to be better able to overcome ecological crises (Raup, 1986; Zhou *et al.*, 2005). More recently, however, Colles *et al.* (2009) showed that different phylogenetic approaches may lead to diverging conclusions. Our present phylogenetic study compares ‘harshness generalists’ to species putatively specialising in habitats lacking any of the harshness factors. The results are consistent with a longer survival of ‘harshness generalists’ and hence rather point towards generalists being, in fact, less susceptible to environmental change than specialists. However, our study also indicates that reduced extinction might possibly be coupled with reduced speciation, as this has been shown with other traits, e.g. geographic range (Parker *et al.*, 1999), leaving practically no net effect on the numbers of species using harsh habitats.

Our results point to a common factor of tolerance of environmental harshness, which would be shared by a pool of low-clade-rank species, as uses of different harsh habitats were positively correlated with one another. This result is not surprising in view of the roles of soil acidity, altitude and latitude: the biologically active part of the soil (the topsoil) becomes more acidic as the decomposition rate of organic matter decreases, leaving the organic matter humified rather than mineralised (Ulrich, 1986; Ponge, 2003, 2012). However, it was more surprising to find relationships between these three factors and drought or metallic pollution. The only point in common among these five factors appears to be a decrease in biological activity caused by harsh environmental conditions. To explain these positive relationships among different types of harshness tolerance, we should first examine the cellular level. The integrity of cell membranes, combined with active cellular repair, is known to protect a wide array of organisms from death caused by environmental hazards (Nriagu, 2003; Oliver *et al.*, 2005; Shi *et al.*, 2008; Timmermans *et al.*, 2009). This feature could be the most primitive mechanism of harshness tolerance, requiring no specialised adaptation to any particular harshness factor but rather the coordinated expression of genes functioning in common in a ‘general-purpose genotype’ (Weider, 1993; Niehrs & Pollet, 1999; Vohradsky *et al.*, 2000; Van Doninck *et al.*, 2002; Kaplan *et al.*, 2004). For instance, it has been shown that drought acclimation produces cold tolerance in springtails (Holmstrup *et al.*, 2002) and that long-chain fatty acids of phospholipidic membranes are involved in this phenomenon (Bayley *et al.*, 2001). These findings are consistent with the evolutionary importance of membrane integrity (Jobson *et al.*, 2010). Adaptation to harsh environments may occur rapidly if a phylogenetic lineage already possesses an efficient array of regulatory genes, known to be as evolutionarily important as changes in enzyme structures (Roelofs *et al.*, 2006, 2010). However, the evolutionary acquisition of this gene array might be difficult and might only occur rarely. This

hypothesis is consistent with our observation of only a few cases of independent acquisitions of the capacity to use harsh habitats.

We showed that derived species of high clade rank were primarily tropical species (while not all tropical species are derived), an observation also made for marine bivalves by Harnik et al. (2010). This result is in contrast to the tropical conservatism hypothesis of Wiens & Donoghue (2004), which suggests that the tropics, representing supposedly more ancient environments, should harbour more ancient species characterised by low clade ranks (without excluding more recent species). Our results could be explained by a more ancient origin of environments observed today outside of the tropics, compared to today's tropical environments (Smith *et al.*, 2007). However, across the lifetime of the Collembola lineage, the tropical environments are usually considered to be at least as old as the non-tropical ones (e.g., Behrensmeyer *et al.*, 1992). Alternatively, our results can be explained if the low clade rank of species results from a trait such as the capacity to use harsh habitats and if species with this trait tend to occur outside rather than inside the tropics. However, we found that the tropical/clade-rank relationship was independent of the use of harsh habitats. The observed high clade ranks of tropical species therefore remain unexplained. Potentially, traits other than the use of harsh habitats need to be considered, as well as an interplay between environmental filters (mainly operating out of the tropics) and evolutionary potential of lineages (mainly operating in the tropics), as postulated by Harnik et al. (2010). We note, however, that most tropical species are found on territories of Gondwanan origin and that the high clade rank of Gondwanan species, in turn, could be explained by their present-day use of mesic habitats. Our results may thus point to a link between niche conservatism, diversification, and biogeographic distribution leading to patterns that are inconsistent with those predicted by Wiens & Donoghue's (2004) tropical conservatism hypothesis. It remains to be tested whether

the patterns we observed are a rare exception for a small group of species or can be found more frequently, e.g., in other groups of invertebrates.

By creating harsh environments (acid rain, polluted water, soil and atmosphere, vegetation-less areas) throughout the world and by accelerating species dispersal (alien introductions), humans select for particular major lineages to the detriment of others (Purvis, 2008; Ozinga *et al.*, 2009; May, 2010). However, our results show that by rendering global environments increasingly harsh, humans also select for particular evolutionary scenarios to the detriment of others: increasingly abundant harsh environments appear to represent museum scenarios, i.e., environments that accumulate low-clade-rank species. It is possible that this outcome is due to low extinction and speciation rates. In contrast, environments of low harshness become rare and therefore potentially represent a cradle scenario, i.e., environments that accumulate high clade-rank species, due perhaps to high rates of speciation. Another result is that the use of harsh habitats is apparently a character that, in most cases, does not originate *de novo* when needed but is carried by particular species for very long periods of time. A high priority should thus be given to the conservation of this pool of low-clade-rank species. However, other studies are necessary to ascertain the generality of the patterns we discerned in one ancient animal group, Collembola. These studies should focus on other ancient but highly diversified groups, such as mites and mosses, which are suspected to be relatively tolerant of harsh environments (Prinzing *et al.*, 2000; Oliver *et al.*, 2005).

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763 **SUPPORTING INFORMATION**

764 **Appendix S1** Phylogenetic reconstruction

765 **Appendix S2** Literature research: definitions, references, exploration of biases

766 **Appendix S3** Robustness of the analysis to variation in underlying phylogenetic trees

767

768 **BIOSKETCH**

769 **Andreas Prinzing** studies the interface of habitat environments, past evolutionary
770 diversification of species pools, and how this diversification controls, and is maintained by,
771 present ecological interactions.

772 Author contributions: JFP and AP conceived the ideas with the collaboration of all other
773 authors, JFP collected the data, CDH constructed the phylogeny, SP analysed the data, and
774 JFP and AP took the lead role in the writing.

775

776 Editor: Melodie McGeoch

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Table 1. Use of harsh environments by *Willemia* species according to literature (references listed in Electronic Appendix S2). See text for more details on stress factors.

	Xeric	Hydric	Arctic	Alpine	Acid	Metallic	Saline	Tolerance breadth (salinity included)	Tolerance breadth (salinity excluded)
<i>W. multilobata</i>	√		√	√	√		√	5	4
<i>W. bellingeri</i>							√	1	0
<i>W. trilobata</i>	√							1	1
<i>W. namibiae</i>	√							1	1
<i>W. similis</i>	√		√	√	√			4	4
<i>W. christianseni</i>				√	√			2	2
<i>W. anophthalma</i>	√	√	√	√	√	√		6	6
<i>W. dubia</i>	√			√	√			3	3
<i>W. scandinavica</i>	√		√	√	√		√	5	4
<i>W. koreana</i>	√							1	1
<i>W. iztacihuatlensis</i>				√	√			2	2
<i>W. bedosae</i>	√							1	1
<i>W. unispina</i>								0	0
<i>W. psammophila</i>							√	1	0
<i>W. virae</i>	√							1	1
<i>W. tali</i>	√							1	1
<i>W. intermedia</i>	√		√	√	√	√		5	5
<i>W. shanghaiensis</i>					√			1	1
<i>W. granulata</i>	√		√	√	√			4	4
<i>W. fjellbergi</i>			√					1	1
<i>W. arida</i>	√		√	√	√			4	4
<i>W. trisphaerae</i>			√	√	√			3	3
<i>W. elisabethum</i>					√			1	1
<i>W. denisi</i>	√	√	√	√	√			5	5
<i>W. japonica</i>								0	0
<i>W. subbulbosa</i>							√	1	0
<i>W. persimilis</i>								0	0
<i>W. acantha</i>								0	0
<i>W. bulbosa</i>								0	0
<i>W. meybolae</i>							√	1	0
<i>W. arenicola</i>							√	1	0
<i>W. nepalensis</i>					√			1	1
<i>W. neocaledonica</i>							√	1	0
<i>W. nadchatrami</i>								0	0
<i>W. brevispina</i>							√	1	0
<i>W. annapurna</i>								0	0
<i>W. buddenbrocki</i>								0	0
<i>W. wandae</i>								0	0
<i>W. nosyboraha</i>							√	1	0
<i>W. delamarei</i>								0	0
<i>W. setonychia</i>								0	0
<i>W. deharvengi</i>							√	1	0

780

FIGURE CAPTIONS

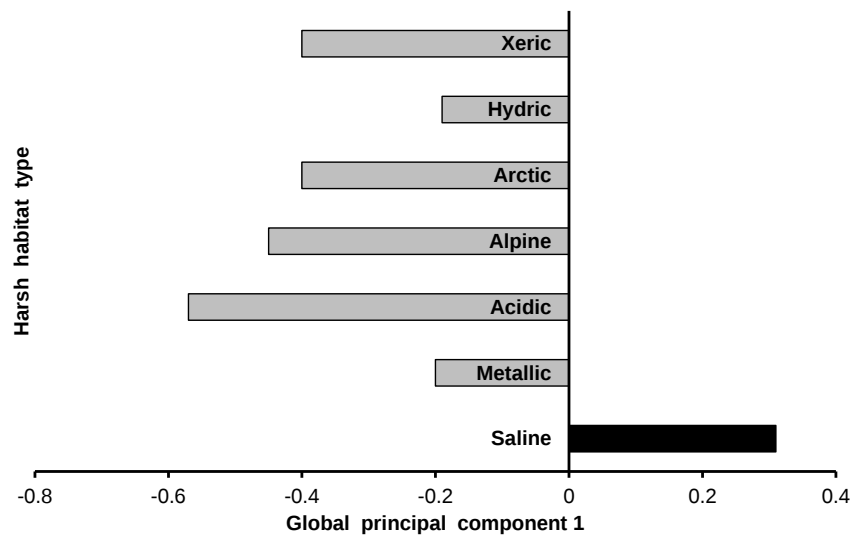
Figure 1. Ordination of correlations between uses of different types of harsh habitats, analysed by pPCA (a multivariate analysis based on phylogenetic distances). The coordinates of harsh habitat types are given along the first principal component. Note that except for salinity, the uses of habitats of all types of harshness are positively correlated.

Figure 2. Parsimony reconstruction of the use of harsh habitats, i.e., any type of harsh habitat used except for salinity (A), tropical distribution (B), and distribution on former Gondwana continents (C). The corresponding character states are shown in black. The tree shapes are not exactly identical because biogeographic distributions could not be assigned to either of the categories for a few species.

Figure 3. Clade ranks of species, i.e., nodal distances to the root, using different numbers of harsh habitat types. Error bar=S.E. Note that species that do not use any harsh habitats are at a greater distance from the root (see text for analyses).

Figure 4. Harshness breadth of species from tropical vs. non-tropical regions (a) and of species of Gondwanan vs. Laurasian origin (b). The few species of intermediate localisation were not included. Error bar=S.E.

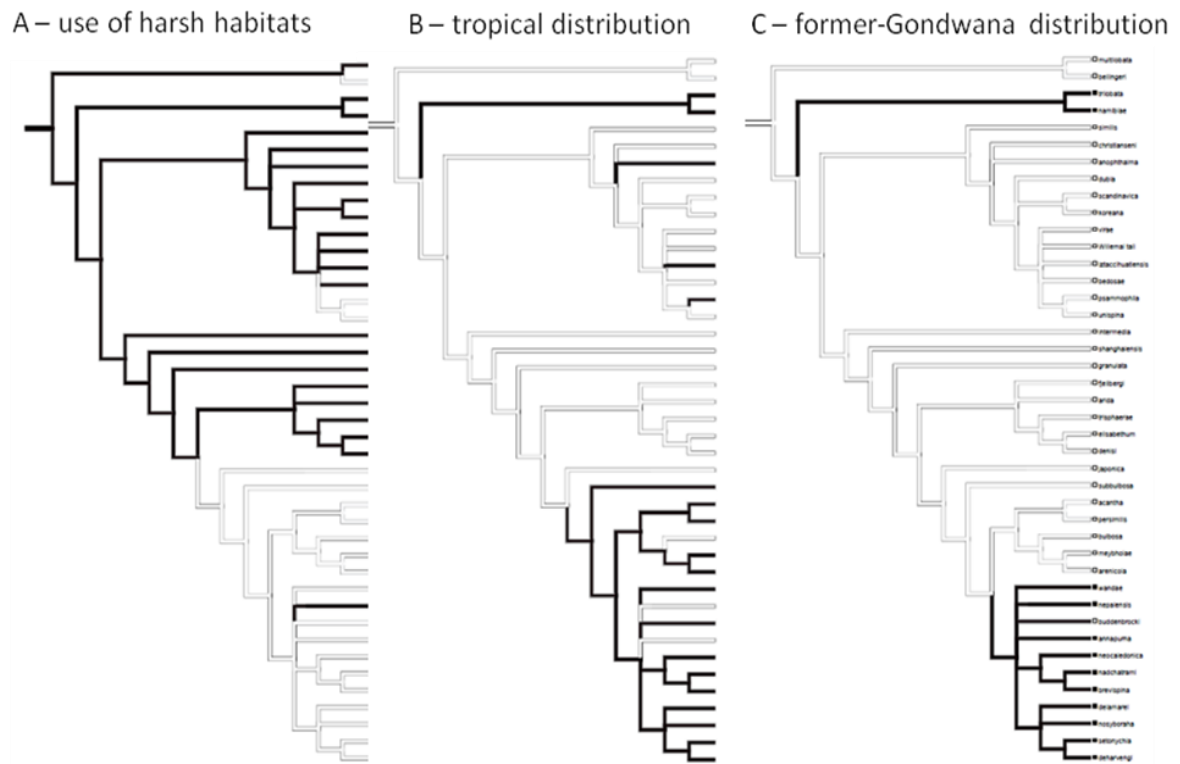
Figure 5. Clade ranks, i.e., distances to the root of the phylogenetic tree, in species from tropical vs. non-tropical regions (a) and from areas of Gondwanan vs. Laurasian origin (b). The few species with intermediate localisation were not included. Error bar=S.E. Note that the difference between Gondwanan vs. Laurasian origin disappears after including harshness breadth as a covariable (whereas harshness breadth is significant at $p=0.011$, see text).

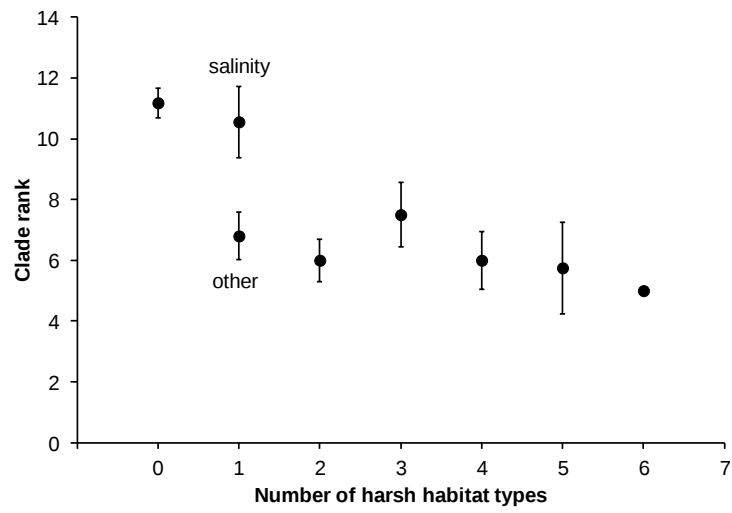


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806 Fig. 1

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813 Fig. 3

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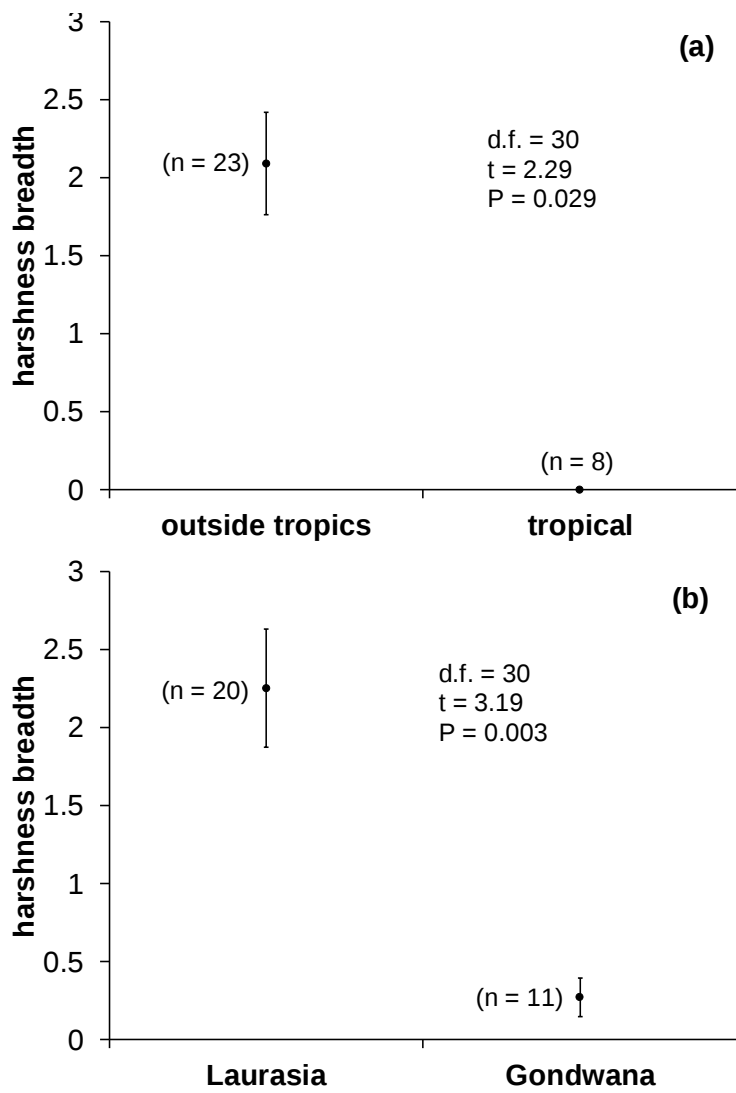


Fig. 4

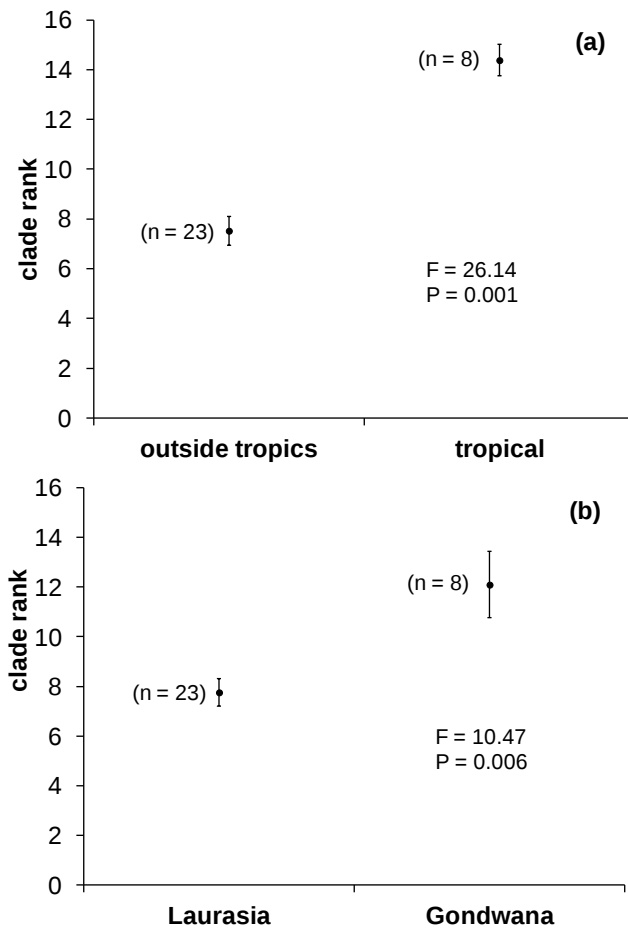


Fig. 5

Appendix S1: Phylogenetic reconstruction

Appendix S1a: General approach

Within the Class Collembola the genus *Willemia* belongs to the Hypogastruridae family. It differs from other hypogastrurid genera by the total lack of pigment and furcula and the small size of the slender body, which never exceeds 1 mm in length (Thibaud, 2004). According to their life form all *Willemia* species belong to the euedaphobiont sub-category Bc3b (small size, slender body, no furcula) of Rusek (2007). The study deals with 42 of the 43 species worldwide known today in this genus (list below in Appendix S1b). The remaining species *W. biseta* Christiansen & Bellinger 1980 was excluded because it could not be studied in detail (see D’Haese 2000). Eight species have been added to the phylogenetic tree published by D’Haese (2000): *W. bulbosa* Bonet 1945, *W. acantha* Bonet 1945, *W. unispina* Fjellberg 2007, *W. iztacihuatlensis* García Gómez & Cutz Pool 2008, *W. tali* Kaprus’ & Nevo 2003, *W. psammophila* Palacios-Vargas & Thibaud 2001, *W. shanghaiensis* Yue 1999, and *W. nosybohara* Thibaud 2008.

Fifty-two morphological characters, which have been detailed in D’Haese (2000), were used for the phylogenetic analysis. Question marks (Appendix S1 b) represent either inapplicable or unknown characters. Autapomorphies, i.e. derived traits that are unique to a given terminal group, were excluded, so that only potentially informative characters were kept. All character states were polarized through comparison with three species belonging to the Hypogastruridae as outgroup: *Hypogastrura vernalis* Carl 1901, *Orogastrura dilatata* Cassagnau 1954, and *Xenylogastrura octocolata* Steiner 1955.

We used morphological characters for reconstructing the phylogeny of the genus *Willemia*, because most species are rare and known only as collection specimens kept in conditions improper for molecular studies, a situation that often impedes worldwide

invertebrate molecular phylogenies if we limit ourselves to molecular characters (Turner et al. 2010). Moreover, it has been shown that phylogenies based on molecular and morphological characters of extant species are in general largely congruent (Jablonski & Finarelli, 2009) despite obvious discrepancies in particular cases. Finally, none of the 52 characters which were used for the phylogeny of the genus *Willemia* (D'Haese, 2000) is related to use of harsh environments. These characters concern chaetotactic setup of body and legs, which is of high taxonomic value in most springtail families (including Hypogastruridae) but has little to do with ecological adaptation (Gisin, 1967; Nayrolles, 1998; Rusek, 2002). The only exception is pigmentation, absent from all *Willemia* species but present in the three outgroup species used (*H. vernalis*, *O. dilatata*, *X. octoculata*). Thus there is no reason to believe that the use of harsh environments, or a set characters correlated with it, was included in the reconstruction of the phylogeny.

The data matrix (Appendix S1b) was analysed with POY version 4.1.2 (Varón *et al.*, 2010) through standard parsimony (static homology) with non-additive character coding (unordered characters). The data matrix was submitted to a thousand replicates, ratchet perturbation i.e. selection of 15% of characters upweighted by a factor of 3 at each iteration (Nixon, 1999), tree fusing (Goloboff, 1999) and to a final branch swapping refinement keeping up to 20% longer trees. Consistency (Kluge & Farris, 1969) and Retention Indices (Farris, 1989) were calculated. Bremer (Bremer, 1988) and jackknife (Farris *et al.*, 1996) branch support indices were computed.

For further calculations on phylogenetic relationships among *Willemia* species we used a strict majority consensus tree based on six fully-resolved trees. The distance of each species to the root was calculated by the number of nodes directly descending from the root to it.

870 All data matrices, character list and analysis scripts can be found below in Appendix S1b and
 871 S1c.

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- 907

915 Appendix S1c: Files used for the construction of the strict consensus phylogenetic tree.

916

917 Printout of files used by Cyrille d'Haese for the construction of the strict consensus phylogenetic tree
 918 (Fig. 1). The file will-bre1.trees needed to calculate bremer support is not provided because of its size
 919 (~58Mo). All these files are available upon request at dhaese@mnhn.fr

920

921 The following file willemia2000.ss is the original data matrix from D'Haese (2000) in Hennig86
 922 format:

```

923 xread
924 'Matrix of DHaese, C. Is psammophily an evolutionary dead end? a
925 phylogenetic test in the genus Willemia (Collembola: Hypogastruridae)
926 Cladistics, 2000, 16, 255-273'
927 52 37
928 Hypogastrura_venalis
929 000000000?0000000000000000000000000000010???000000
930 Orogastrura_dilatata
931 000000000000000000000000000000000000101000101000??000
932 Xenyllogastrura_octoculata
933 00000001000?0100000001011000000000000010010?1000?0000
934 Willemia_annapurna
935 1003003111113111013100133101000110111111110111111101
936 Willemia_anophthalma
937 1000000110001011010100011101000100010100010000100001
938 Willemia_arenicola
939 0222222111102111012101023100001111111110110100111001
940 Willemia_arida
941 1332222110?100110101000??101000110000110110101100011
942 Willemia_bedosae
943 1000000110001011010100011101000110110100110000100001
944 Willemia_bellingeri
945 0000020110010011010100011100000000000000010100100001
946 Willemia_brevispina
947 130320311111311111010012210100011011111111111111101
948 Willemia_buddenbrocki
949 1003003111113111112100133101000110111111110111111101
950 Willemia_christianseni
951 1300000110001011010100011101000110010100010000100001
952 Willemia_deharvengi
953 2003003111113111013100123111110110111111110111111111
954 Willemia_delamarei
955 100300311????1110121001??111110110111111111????1???01
956 Willemia_denisi
957 1111111110010011110101011101001110111110110101100011
958 Willemia_dubia
959 1000000110001011010100011101000110110100010000100001
960 Willemia_elisabethum
961 1111211110010011110101011101001110111110110101100011
962 Willemia_fjellbergi
963 133222211001001101010001110100011000011011?1?1100011

```

```

964 Willemia_granulata
965     1000220110010011010100011101000110000110110100100011
966 Willemia_intermedia
967     1300000110010011010100011101000110000110110100100001
968 Willemia_japonica
969     1002222110010011010100011101000110010110110100100011
970 Willemia_koreana
971     1000220110001011010100011101000110110100010000100001
972 Willemia_meybholae
973     0222222111112111013101023100001111111110110100111011
974 Willemia_multilobata
975     00000201100100??0101000111000000000000000010100100001
976 Willemia_nadchatrami
977     10030031111131111010012210000011011111?0111111??101
978 Willemia_namibiae
979     0000000110011011010?1?02310000010011010000?100100?01
980 Willemia_neocaledonica
981     10030031111131111210012210100011011111111111111101
982 Willemia_nepalensis
983     100300311111311101210012211100011011111111011111101
984 Willemia_persimilis
985     0300220111?120110121010??101001110111110110100111001
986 Willemia_scandinavica
987     100022011000101101010001110?000110110100010000100001
988 Willemia_setonychia
989     200300311????11101310????11111011011111111????1???11
990 Willemia_similis
991     1000000110011011010100011101000010010100010000100001
992 Willemia_subbulbosa
993     1222222111112011010100023101000110010110110100111001
994 Willemia_trilobata
995     0000000110011011010?1002310000010011010000?1001???01
996 Willemia_trisphaerae
997     1311221110010011?10100011101000110000110110101100011
998 Willemia_virae
999     100000011000101101010001110100011011110011?000100001
1000 Willemia_wandae
1001     10030031111131111210013311100011011111111111111101
1002 ;
1003 ccode - 0.51;
1004 proc /;
1005 ;
1006 cn
1007 {0 On_antennal_segment_IV, apical_vesicle large small absent;
1008 {1 Sensilla_e1_on_antennal_segment_IV subcylindrical_(Figs._2A_and_2D)
1009 candle_flame-shaped_(Fig._2B) globular_(Fig._2C)
1010 not_differentiated_from_ordinary_setae;
1011 {2 Sensilla_e2_on_antennal_segment_IV subcylindrical_(Figs._2A_and_2D)
1012 candle_flame-shaped_(Fig._2B) globular_(Fig._2C)
1013 not_differentiated_from_ordinary_setae;
1014 {3 Sensilla_e3_on_antennal_segment_IV subcylindrical_(Fig._2A)
1015 candle_flame-shaped_(Fig._2B) globular_(Fig._2C)
1016 globular_in_cavity_(Fig._2D);
1017 {4 Sensilla_d_on_antennal_segment_IV subcylindrical_(Figs._2A_and_2D)
1018 candle_flame-shaped_not_differentiated_from_ordinary_setae_(Fig._2C);
1019 {5 Sensilla_i1_on_antennal_segment_IV subcylindrical_(Figs._2A_and_2D)
1020 candle_flame-shaped_(Fig._2B)
1021 not_differentiated_from_ordinary_setae_(Fig._2C);

```

1022 {6 Sensilla_i2_on_antennal_segment_IV subcylindrical_(Fig._2A)
 1023 candle_flame-shaped_(Fig._2B) globular_(Fig._2C)
 1024 globular_in_cavity_(Fig._2D);
 1025 {7
 1026 Small_internal_sensilla_of_sensory organ_of_antennal_segment_III_(Figs.
 1027 _2A_to_2D) free covered_in_part_by_a_tegumental_fold;
 1028 {8 Third_and_fourth_antennal_segments clearly_separated
 1029 ventrally_slightly_fused;
 1030 {9 Antennal_segment_II_with 12_setae 11_setae;
 1031 {10 Antennal_segment_I_with 7_setae 6_setae;
 1032 {11 Prelabral_chaetotaxy_with 4_setae 2_setae;
 1033 {12 Labral_chaetotaxy_with 5.5.4_setae 4.5.4_setae 2.5.4_setae
 1034 5.3.4_setae;
 1035 {13 Seta_a0_on_the_head present_(Fig._1A) absent_(Fig._1B);
 1036 {14 Number_of_setae_d_on_the_head: 5+_5 4+_4_(Figs._1A_and_1B);
 1037 {15 Number_of_setae_v_on_the_head: 2+_2 1+_1_(Figs._1A_and_1B);
 1038 {16 Setae_c1_on_the_head present absent;
 1039 {17 Corneules present absent;
 1040 {18 Postantennal_organ_with 4_to_9_vesicles_(Fig._1A) 10_to_15_vesicles
 1041 more_than_15_vesicles_(Fig._1B);
 1042 {19 Setae_al_of_thoracic_tergum_III_positioned on_thoracic_tergum_III
 1043 between_thoracic_terga_II_and_III_(Figs._1A_and_1B);
 1044 {20 On_second_and_third_thoracic_terga,_setae_al present absent;
 1045 {21 On_thoracic_terga_II_and_III,_setae_a2 present absent;
 1046 {22 On_thoracic_terga_II_and_III,_setae_m3 present_(Fig._1A)
 1047 absent_(Fig._1B);
 1048 {23 Tibiotarsi_I_and_II_with 19_setae 17_setae 12_setae 11_setae;
 1049 {24 Tibiotarsus_III_with 18_setae 16_setae 12_setae 11_or_10_setae;
 1050 {25 Tibiotarsi_with_tenant_hair without_tenant_hair;
 1051 {26 On_thoracic_tergum_III,_setae_s(=m7) subcylindrical_and_acuminate
 1052 lanceolate;
 1053 {27 On_abdominal_terga_II_and_III,_setae_s
 1054 subcylindrical_and_acuminate_(Fig._1A) lanceolate_(Fig._1B);
 1055 {28 On_abdominal_tergum_IV,_setae_s subcylindrical_and_acuminate
 1056 lanceolate;
 1057 {29 On_abdominal_tergum_V,_setae_s subcylindrical_and_acuminate
 1058 lanceolate;
 1059 {30 On_abdominal_terga_II_and_III,_setae_a2 present absent;
 1060 {31 On_abdominal_terga_II_and_III,_setae_m2 present_(Fig._1A)
 1061 absent_(Fig._1B);
 1062 {32 On_abdominal_terga_II_and_III,_setae_m3 present absent;
 1063 {33 On_abdominal_terga_I_II_and_III,_tegumentary_granulation normal
 1064 coarse_secondary_granulation_near_setae_s;
 1065 {34 On_abdominal_tergum_IV,_setae_m1 present_(Fig._1A)
 1066 absent_(Fig._1B);
 1067 {35 On_abdominal_tergum_IV,_setae_m2 present absent;
 1068 {36 On_abdominal_tergum_IV,_setae_m3 present_(Fig._1A)
 1069 absent_(Fig._1B);
 1070 {37 On_abdominal_tergum_IV,_setae_m3' present absent;
 1071 {38 On_abdominal_tergum_IV,_setae_p5 present_(Fig._1A)
 1072 absent_(Fig._1B);
 1073 {39 On_abdominal_tergum_V,_setae_a3 present_(Fig._1A) absent_(Fig._1B);
 1074 {40 On_abdominal_tergum_V,_setae_s
 1075 in_p3_position_i.e._p2_present_(Fig._1A)
 1076 in_p2_position_i.e._p2_absent_(Fig._1B);
 1077 {41 Ventral_tube_with_more_than_4+_4_setae with_4_1_4_setae;
 1078 {42 On_abdominal_sternum_II,_setae_a3 present absent;

```
1079 {43 On_abdominal_sternum_IV,_setae_a1 present_(Fig._3A)
1080 absent_(Fig._3B);
1081 {44 On_abdominal_sternum_IV, 4_rows_of_setae_(Fig._3A)
1082 3_rows_of_setae_(Fig._3B);
1083 {45 On_abdominal_sternum_IV,_setae_m1 present absent;
1084 {46 Furca present absent;
1085 {47 On_anal_lobes,_setae_e present_(Fig._4A) absent_(Fig._4B);
1086 {48 On_anal_lobes,_setae_z present_(Fig._4A) absent_(Fig._4B);
1087 {49 On_anal_lobes,_distal_setae_of_hr_group present_(Fig._4A)
1088 absent_(Fig._4B);
1089 {50 Anal_spines present absent;
1090 {51 Pigmentation present absent;
1091 ;
1092
1093
```

1094 The following file willemia2011_char.ss is the new matrix with 5 Willemia species added along with
1095 the character list:

```

1096 xread
1097 ' Matrix of Ponge et al based on DHaese 2000 (Is psammophily an
1098 evolutionary dead end? Cladistics) with new species added '
1099 52 45
1100 Hypogastrura_vernalis
1101 000000000?0000000000000000000000000000010???000000
1102 Orogastrura_dilatata
1103 000000000000000000000000000000000000101000101000??000
1104 Xenyllogastrura_octoculata
1105 00000001000?0100000001011000000000000010010?1000?0000
1106 Willemia_annapurna
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1109 1000000110001011010100011101000100010100010000100001
1110 Willemia_arenicola
1111 0222222111102111012101023100001111111110110100111001
1112 Willemia_nosyboraha
1113 10030031111??111111100133111110110111111110010????01
1114 Willemia_arida 1332222110?100110101000??101000110000110110101100011
1115 Willemia_bedosae 1000000110001011010100011101000110110100110000100001
1116 Willemia_bellingeri
1117 0000020110010011010100011100000000000000010100100001
1118 Willemia_brevispina
1119 130320311111311111010012210100011011111111111111101
1120 Willemia_buddenbrocki
1121 1003003111113111112100133101000110111111110111111101
1122 Willemia_christianseni
1123 1300000110001011010100011101000110010100010000100001
1124 Willemia_deharvengi
1125 2003003111113111013100123111110110111111110111111111
1126 Willemia_delamarei
1127 100300311????1110121001??11111011011111111????1???01
1128 Willemia_denisi 111111110010011110101011101001110111110110101100011
1129 Willemia_dubia 1000000110001011010100011101000110110100010000100001
1130 Willemia_elisabethum
1131 1111211110010011110101011101001110111110110101100011
1132 Willemia_fjellbergi
1133 133222211001001101010001110100011000011011?1?1100011
1134 Willemia_unispinal00000001??10011?101000111111101101101001100001??011
1135 Willemia_granulata
1136 1000220110010011010100011101000110000110110100100011
1137 Willemia_intermedia
1138 1300000110010011010100011101000110000110110100100001
1139 Willemia_iztaccihuatlensis 11000001100010110101000[1-2][1-
1140 2]1010011101101?01100?0100001
1141 Willemia_japonica1002222110010011010100011101000110010110110100100011
1142 Willemia_koreana 1000220110001011010100011101000110110100010000100001
1143 Willemia_meybholae
1144 0222222111112111013101023100001111111110110100111011
1145 Willemia_multilobata
1146 00000201100100??0101000111000000000000000010100100001
1147 Willemia_nadchatrami
1148 100300311111311111010012210000011011111?0111111??101
1149 Willemia_namibiae0000000110011011010?1?02310000010011010000?100100?01

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```

1150 Willemia_neocaledonica
1151     10030031111131111121001221010001101111111111111111101
1152 Willemia_nepalensis
1153     10030031111131110121001221110001101111111110111111101
1154 Willemia_persimilis
1155     0300220111?120110121010??1010011101111110110100111001
1156 Willemia_psammophila
1157     00000001110010110111000331111101000101?01100001?0001
1158 Willemia_bulbosa 0322222111?1201101[0-
1159 1]1010??101001110111110110100111001
1160 Willemia_acantha 0300220111?120110121010??101001110111110110100111011
1161 Willemia_scandinavica
1162     100022011000101101010001110?000110110100010000100001
1163 Willemia_setonychia
1164     200300311????11101310????111110110111111111????1???11
1165 Willemia_shanghaiensis
1166     100022011???????101000??100000110000??011????1??001
1167 Willemia_similis 1000000110011011010100011101000010010100010000100001
1168 Willemia_subbulbosa
1169     1222222111112011010100023101000110010110110100111001
1170 Willemia_tali     1111?01110001011010100011111000110111100110000110001
1171 Willemia_trilobata
1172     0000000110011011010?1002310000010011010000?1001???01
1173 Willemia_trisphaerae
1174     1311221110010011?10100011101000110000110110101100011
1175 Willemia_virae    100000011000101101010001110100011011110011?000100001
1176 Willemia_wandae   1003003111113111112100133111000110111111111111111101
1177 ;
1178
1179 ccode - 0.51;
1180 proc/;
1181
1182 ;
1183 cn
1184 {0 On_antennal_segment_IV, apical_vesicle large small absent;
1185 {1 Sensilla_e1_on_antennal_segment_IV subcylindrical_(Figs._2A_and_2D)
1186 candle_flame-shaped_(Fig._2B) globular_(Fig._2C)
1187 not_differentiated_from_ordinary_setae;
1188 {2 Sensilla_e2_on_antennal_segment_IV subcylindrical_(Figs._2A_and_2D)
1189 candle_flame-shaped_(Fig._2B) globular_(Fig._2C)
1190 not_differentiated_from_ordinary_setae;
1191 {3 Sensilla_e3_on_antennal_segment_IV subcylindrical_(Fig._2A)
1192 candle_flame-shaped_(Fig._2B) globular_(Fig._2C)
1193 globular_in_cavity_(Fig._2D);
1194 {4 Sensilla_d_on_antennal_segment_IV subcylindrical_(Figs._2A_and_2D)
1195 candle_flame-shaped not_differentiated_from_ordinary_setae_(Fig._2C);
1196 {5 Sensilla_i1_on_antennal_segment_IV subcylindrical_(Figs._2A_and_2D)
1197 candle_flame-shaped_(Fig._2B)
1198 not_differentiated_from_ordinary_setae_(Fig._2C);
1199 {6 Sensilla_i2_on_antennal_segment_IV subcylindrical_(Fig._2A)
1200 candle_flame-shaped_(Fig._2B) globular_(Fig._2C)
1201 globular_in_cavity_(Fig._2D);
1202 {7
1203 Small_internal_sensilla_of_sensory_organ_of_antennal_segment_III_(Figs.
1204 _2A_to_2D) free covered_in_part_by_a_tegumental_fold;
1205 {8 Third_and_fourth_antennal_segments clearly_separated
1206 ventrally_slightly_fused;
1207 {9 Antennal_segment_II_with 12_setae 11_setae;

```

1208 {10 Antennal_segment_I_with 7_setae 6_setae;
 1209 {11 Prelabral_chaetotaxy_with 4_setae 2_setae;
 1210 {12 Labral_chaetotaxy_with 5.5.4_setae 4.5.4_setae 2.5.4_setae
 1211 5.3.4_setae;
 1212 {13 Seta_a0_on_the_head present_(Fig._1A) absent_(Fig._1B);
 1213 {14 Number_of_setae_d_on_the_head: 5+_5 4+_4_(Figs._1A_and_1B);
 1214 {15 Number_of_setae_v_on_the_head: 2+_2 1+_1_(Figs._1A_and_1B);
 1215 {16 Setae_cl_on_the_head present absent;
 1216 {17 Corneules present absent;
 1217 {18 Postantennal_organ_with 4_to_9_vesicles_(Fig._1A) 10_to_15_vesicles
 1218 more_than_15_vesicles_(Fig._1B);
 1219 {19 Setae_al_of_thoracic_tergum_III_positioned_on_thoracic_tergum_III
 1220 between_thoracic_terga_II_and_III_(Figs._1A_and_1B);
 1221 {20 On_second_and_third_thoracic_terga,_setae_al present absent;
 1222 {21 On_thoracic_terga_II_and_III,_setae_a2 present absent;
 1223 {22 On_thoracic_terga_II_and_III,_setae_m3 present_(Fig._1A)
 1224 absent_(Fig._1B);
 1225 {23 Tibiotarsi_I_and_II_with 19_setae 17_setae 12_setae 11_setae;
 1226 {24 Tibiotarsus_III_with 18_setae 16_setae 12_setae 11_or_10_setae;
 1227 {25 Tibiotarsi_with_tenant_hair without_tenant_hair;
 1228 {26 On_thoracic_tergum_III,_setae_s_(=m7) subcylindrical_and_acuminate
 1229 lanceolate;
 1230 {27 On_abdominal_terga_II_and_III,_setae_s
 1231 subcylindrical_and_acuminate_(Fig._1A) lanceolate_(Fig._1B);
 1232 {28 On_abdominal_tergum_IV,_setae_s subcylindrical_and_acuminate
 1233 lanceolate;
 1234 {29 On_abdominal_tergum_V,_setae_s subcylindrical_and_acuminate
 1235 lanceolate;
 1236 {30 On_abdominal_terga_II_and_III,_setae_a2 present absent;
 1237 {31 On_abdominal_terga_II_and_III,_setae_m2 present_(Fig._1A)
 1238 absent_(Fig._1B);
 1239 {32 On_abdominal_terga_II_and_III,_setae_m3 present absent;
 1240 {33 On_abdominal_terga_I_II_and_III,_tegumentary_granulation normal
 1241 coarse_secondary_granulation_near_setae_s;
 1242 {34 On_abdominal_tergum_IV,_setae_m1 present_(Fig._1A)
 1243 absent_(Fig._1B);
 1244 {35 On_abdominal_tergum_IV,_setae_m2 present absent;
 1245 {36 On_abdominal_tergum_IV,_setae_m3 present_(Fig._1A)
 1246 absent_(Fig._1B);
 1247 {37 On_abdominal_tergum_IV,_setae_m3' present absent;
 1248 {38 On_abdominal_tergum_IV,_setae_p5 present_(Fig._1A)
 1249 absent_(Fig._1B);
 1250 {39 On_abdominal_tergum_V,_setae_a3 present_(Fig._1A) absent_(Fig._1B);
 1251 {40 On_abdominal_tergum_V,_setae_s
 1252 in_p3_position_i.e._p2_present_(Fig._1A)
 1253 in_p2_position_i.e._p2_absent_(Fig._1B);
 1254 {41 Ventral_tube_with_more_than_4+_4_setae_with_4_1_4_setae;
 1255 {42 On_abdominal_sternum_II,_setae_a3 present absent;
 1256 {43 On_abdominal_sternum_IV,_setae_a1 present_(Fig._3A)
 1257 absent_(Fig._3B);
 1258 {44 On_abdominal_sternum_IV, 4_rows_of_setae_(Fig._3A)
 1259 3_rows_of_setae_(Fig._3B);
 1260 {45 On_abdominal_sternum_IV,_setae_m1 present absent;
 1261 {46 Furca present absent;
 1262 {47 On_anal_lobes,_setae_e present_(Fig._4A) absent_(Fig._4B);
 1263 {48 On_anal_lobes,_setae_z present_(Fig._4A) absent_(Fig._4B);
 1264 {49 On_anal_lobes,_distal_setae_of_hr_group present_(Fig._4A)
 1265 absent_(Fig._4B);

```
1266 {50 Anal_spines present absent;  
1267 {51 Pigmentation present absent;  
1268 ;  
1269  
1270
```

1271 The following file willemia2011.ss is the same data matrix but without the character list to be directly
1272 readable by POY:

```

1273 xread
1274 ' Matrix of Ponge et al based on DHaese 2000 (Is psammophily an
1275 evolutionary dead end? Cladistics) with new species added '
1276 52 45
1277 Hypogastrura_vernalis
1278 000000000?0000000000000000000000000000010???000000
1279 Orogastrura_dilatata
1280 000000000000000000000000000000000000101000101000??000
1281 Xenyllogastrura_octoculata
1282 00000001000?0100000001011000000000000010010?1000?0000
1283 Willemia_annapurna
1284 1003003111113111013100133101000110111111110111111101
1285 Willemia_anophthalma
1286 1000000110001011010100011101000100010100010000100001
1287 Willemia_arenicola
1288 0222222111102111012101023100001111111110110100111001
1289 Willemia_nosyboraha
1290 10030031111??111111100133111110110111111110010????01
1291 Willemia_arida 1332222110?100110101000??101000110000110110101100011
1292 Willemia_bedosae 1000000110001011010100011101000110110100110000100001
1293 Willemia_bellingeri
1294 0000020110010011010100011100000000000000010100100001
1295 Willemia_brevispina
1296 130320311111311111010012210100011011111111111111101
1297 Willemia_buddenbrocki
1298 1003003111113111112100133101000110111111110111111101
1299 Willemia_christianseni
1300 1300000110001011010100011101000110010100010000100001
1301 Willemia_deharvengi
1302 2003003111113111013100123111110110111111110111111111
1303 Willemia_delamarei
1304 100300311????1110121001??11111011011111111????1???01
1305 Willemia_denisi 1111111110010011110101011101001110111110110101100011
1306 Willemia_dubia 1000000110001011010100011101000110110100010000100001
1307 Willemia_elisabethum
1308 1111211110010011110101011101001110111110110101100011
1309 Willemia_fjellbergi
1310 133222211001001101010001110100011000011011?1?1100011
1311 Willemia_unispinal100000001??10011?101000111111101101101001100001??011
1312 Willemia_granulata
1313 1000220110010011010100011101000110000110110100100011
1314 Willemia_intermedia
1315 1300000110010011010100011101000110000110110100100001
1316 Willemia_iztaccihuatlensis 11000001100010110101000[1-2][1-
1317 2]1010011101101?01100?0100001
1318 Willemia_japonica1002222110010011010100011101000110010110110100100011
1319 Willemia_koreana 1000220110001011010100011101000110110100010000100001
1320 Willemia_meybholae
1321 0222222111112111013101023100001111111110110100111011
1322 Willemia_multilobata
1323 00000201100100??0101000111000000000000000010100100001
1324 Willemia_nadchatrami
1325 100300311111311111010012210000011011111?0111111??101
1326 Willemia_namibiae0000000110011011010?1?02310000010011010000?100100?01

```

```

1327 Willemia_neocaledonica
1328     100300311111311111210012210100011011111111111111101
1329 Willemia_nepalensis
1330     100300311111311101210012211100011011111111011111101
1331 Willemia_persimilis
1332     0300220111?120110121010??101001110111110110100111001
1333 Willemia_psammophila
1334     00000001110010110111000331111101000101?01100001?0001
1335 Willemia_bulbosa 0322222111?1201101[0-
1336 1]1010??101001110111110110100111001
1337 Willemia_acantha 0300220111?120110121010??101001110111110110100111011
1338 Willemia_scandinavica
1339     100022011000101101010001110?000110110100010000100001
1340 Willemia_setonychia
1341     200300311????11101310????111110110111111111????1???11
1342 Willemia_shanghaiensis
1343     100022011???????101000??100000110000??011????1???001
1344 Willemia_similis 1000000110011011010100011101000010010100010000100001
1345 Willemia_subbulbosa
1346     1222222111112011010100023101000110010110110100111001
1347 Willemia_tali     1111?01110001011010100011111000110111100110000110001
1348 Willemia_trilobata
1349     0000000110011011010?1002310000010011010000?1001???01
1350 Willemia_trisphaerae
1351     1311221110010011?10100011101000110000110110101100011
1352 Willemia_virae     100000011000101101010001110100011011110011?000100001
1353 Willemia_wandae     100300311111311111210013311100011011111111111111101
1354 ;
1355
1356 ccode - 0.51;
1357 proc/;
1358
1359
1360
1361

```

1362 The following file will.sh is the main analysis script for POY:

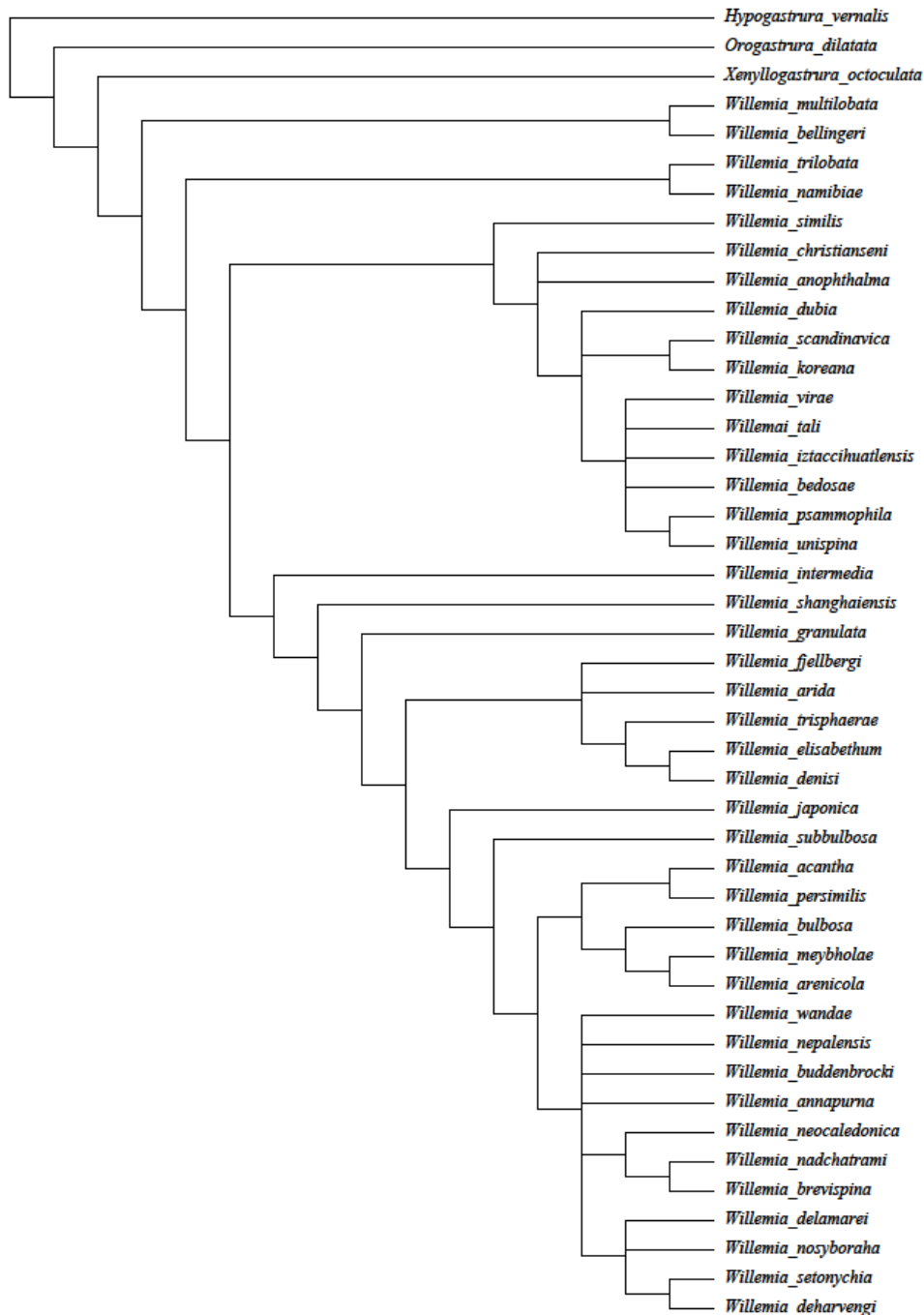
```
1363 wipe ()
1364 read ("willemia2011.ss")
1365 set (root: "Hypogastrura_vernalis")
1366 build (1000)
1367 select (unique)
1368 perturb (iterations:2, ratchet:(0.15,3), swap(tbr, trees:2))
1369 select (unique)
1370 fuse ()
1371 select (unique)
1372 swap (threshold:20)
1373 swap (all, visited:"will-brel.trees", timeout:3600)
1374 select ()
1375 report ("will.tre", trees:(total))
1376 report ("will_results.ss", phastwinclad, trees:(hennig, total))
1377 report ("will-cons.tre", consensus, "will-cons", graphconsensus)
1378 report ("will-stats.txt", treestats, ci, ri)
1379 report ("will-diag.txt", diagnosis)
1380 exit ()
1381
1382
1383
```

1384 will-cons.pdf (consensus in pdf format), will-cons.tre (consensus in text format), will-stats (tree length
 1385 ci and ri), and will.tre (the six equally parsimonious trees) are the results of the analysis.

1386

1387 will-cons.pdf:

Strict Majority Consensus Tree



1388

1389

1390 will-cons.tre:

1391 Strict Majority Consensus Tree

1392 (Hypogastrura_vernalis,(Orogastrura_dilatata,(Xenyllogastrura_octoculat
1393 a,((Willemia_multilobata,Willemia_bellingeri),((Willemia_trilobata,Will
1394 emia_namibiae),((Willemia_similis,(Willemia_christianseni,Willemia_anop
1395 hthalma,(Willemia_dubia,(Willemia_scandinavica,Willemia_koreana),(Wille
1396 mia_virae,Willemai_tali,Willemia_iztaccihuatlensis,Willemia_bedosae,(Wi
1397 llemia_psammophila,Willemia_unispina))))), (Willemia_intermedia,(Willemi
1398 a_shanghaiensis,(Willemia_granulata,((Willemia_fjellbergi,Willemia_arid
1399 a,(Willemia_trisphaerae,(Willemia_elisabethum,Willemia_denisi))), (Wille
1400 mia_japonica,(Willemia_subbulbosa,(((Willemia_acantha,Willemia_persimil
1401 is),(Willemia_bulbosa,(Willemia_meybholae,Willemia_arenicola))), (Willem
1402 ia_wandae,Willemia_nepalensis,Willemia_buddenbrocki,Willemia_annapurna,
1403 (Willemia_neocaledonica,(Willemia_nadchatrami,Willemia_brevispina)), (Wi
1404 llemia_delamarei,Willemia_nosyboraha,(Willemia_setonychia,Willemia_deha
1405 rvengi)))))))))

1406

1407

```

1408 will-stats:
1409 Trees Found:
1410
1411             Tree length      Number of hits
1412             154.              6
1413 CI Statistics:
1414
1415             Tree Cost CI
1416             154.          46.1038961039
1417             154.          46.1038961039
1418             154.          46.1038961039
1419             154.          46.1038961039
1420             154.          46.1038961039
1421             154.          46.1038961039
1422 RI Statistics:
1423
1424             Tree Cost RI
1425             154.          82.3404255319
1426             154.          82.3404255319
1427             154.          82.3404255319
1428             154.          82.3404255319
1429             154.          82.3404255319
1430             154.          82.3404255319
1431
1432

```

1433 will.tre:

```

1434 (Hypogastrura_venalis, (Orogastrura_dilatata, (Xenyllogastrura_octoculat
1435 a
1436 , ((Willemia_multilobata, Willemia_bellingeri), ((Willemia_trilobata
1437 , Willemia_namibiae), ((Willemia_similis, ((Willemia_christianseni
1438 , Willemia_anophthalma), ((Willemia_dubia, (Willemia_scandinavica
1439 , Willemia_koreana))), (Willemia_iztaccihuatlensis, (Willemia_bedosae
1440 , ((Willemia_unispina, Willemia_psammophila), (Willemia_virae, Willemia_tal
1441 i))))))
1442 ), (Willemia_intermedia, (Willemia_shanghaiensis, (Willemia_granulata
1443 , (((Willemia_fjellbergi, Willemia_arida), (Willemia_trisphaerae
1444 , (Willemia_elisabethum, Willemia_denisi))), (Willemia_japonica
1445 , (Willemia_subbulbosa, (((Willemia_persimilis, Willemia_acantha)
1446 , (Willemia_bulbosa, (Willemia_meybholae, Willemia_arenicola))))
1447 , ((Willemia_nepalensis, (Willemia_neocaledonica, (Willemia_nadchatrami
1448 , Willemia_brevispina))), (Willemia_annapurna, (Willemia_buddenbrocki
1449 , (Willemia_wandae, (Willemia_nosyboraha, (Willemia_delamarei
1450 , (Willemia_setonychia, Willemia_deharvengi))))))))) [154.];
1451 (Hypogastrura_venalis, (Orogastrura_dilatata, (Xenyllogastrura_octoculat
1452 a
1453 , ((Willemia_multilobata, Willemia_bellingeri), ((Willemia_trilobata
1454 , Willemia_namibiae), ((Willemia_similis, ((Willemia_christianseni
1455 , Willemia_anophthalma), ((Willemia_dubia, (Willemia_scandinavica
1456 , Willemia_koreana))), (Willemia_virae, (Willemia_unispina, Willemia_psammo
1457 phila)
1458 ), (Willemia_bedosae, (Willemia_iztaccihuatlensis, Willemia_tali))))))
1459 , (Willemia_intermedia, (Willemia_shanghaiensis, (Willemia_granulata
1460 , (((Willemia_fjellbergi, Willemia_arida), (Willemia_trisphaerae
1461 , (Willemia_elisabethum, Willemia_denisi))), (Willemia_japonica
1462 , (Willemia_subbulbosa, (((Willemia_persimilis, Willemia_acantha)
1463 , (Willemia_bulbosa, (Willemia_meybholae, Willemia_arenicola))))
1464 , ((Willemia_nepalensis, (Willemia_neocaledonica, (Willemia_nadchatrami
1465 , Willemia_brevispina))), (Willemia_annapurna, (Willemia_buddenbrocki
1466 , (Willemia_wandae, (Willemia_nosyboraha, (Willemia_delamarei
1467 , (Willemia_setonychia, Willemia_deharvengi))))))))) [154.];
1468 (Hypogastrura_venalis, (Orogastrura_dilatata, (Xenyllogastrura_octoculat
1469 a
1470 , ((Willemia_multilobata, Willemia_bellingeri), ((Willemia_trilobata
1471 , Willemia_namibiae), ((Willemia_similis, (Willemia_christianseni
1472 , (Willemia_anophthalma, (Willemia_dubia, ((Willemia_scandinavica
1473 , Willemia_koreana), ((Willemia_unispina, Willemia_psammophila)
1474 , (Willemia_bedosae, (Willemia_iztaccihuatlensis, (Willemia_virae, Willemia
1475 _tali)
1476 ))))))), (Willemia_intermedia, (Willemia_shanghaiensis, (Willemia_granula
1477 ta
1478 , ((Willemia_fjellbergi, (Willemia_arida, (Willemia_trisphaerae
1479 , (Willemia_elisabethum, Willemia_denisi))), (Willemia_japonica
1480 , (Willemia_subbulbosa, (((Willemia_persimilis, Willemia_acantha)
1481 , (Willemia_bulbosa, (Willemia_meybholae, Willemia_arenicola))))
1482 , ((Willemia_nepalensis, ((Willemia_nosyboraha, Willemia_delamarei)
1483 , (Willemia_setonychia, Willemia_deharvengi))), (Willemia_annapurna
1484 , (Willemia_buddenbrocki, (Willemia_wandae, (Willemia_neocaledonica
1485 , (Willemia_nadchatrami, Willemia_brevispina))))))))) [154.];
1486 (Hypogastrura_venalis, (Orogastrura_dilatata, (Xenyllogastrura_octoculat
1487 a
1488 , ((Willemia_multilobata, Willemia_bellingeri), ((Willemia_trilobata
1489 , Willemia_namibiae), ((Willemia_similis, (Willemia_christianseni

```

1490 , (Willemia_anophthalma, ((Willemia_scandinavica, Willemia_koreana)
 1491 , (Willemia_dubia, ((Willemia_unispina, Willemia_psammophila), (Willemia_vi
 1492 rae
 1493 , (Willemia_bedosae, (Willemia_iztaccihuatlensis, Willemia_tali))))))
 1494 , (Willemia_intermedia, (Willemia_shanghaiensis, (Willemia_granulata
 1495 , ((Willemia_fjellbergi, Willemia_arida), (Willemia_trisphaerae
 1496 , (Willemia_elisabethum, Willemia_denisi))), (Willemia_japonica
 1497 , (Willemia_subbulbosa, ((Willemia_persimilis, Willemia_acantha)
 1498 , (Willemia_bulbosa, (Willemia_meybholae, Willemia_arenicola)))
 1499 , ((Willemia_nepalensis, ((Willemia_nosyboraha, Willemia_delamarei)
 1500 , (Willemia_setonychia, Willemia_deharvengi))), (Willemia_annapurna
 1501 , (Willemia_buddenbrocki, (Willemia_wandae, (Willemia_neocaledonica
 1502 , (Willemia_nadchatrami, Willemia_brevispina))))))))) [154.];
 1503 (Hypogastrura_vernalis, (Orogastrura_dilatata, (Xenyllogastrura_octoculat
 1504 a
 1505 , ((Willemia_multilobata, Willemia_bellingeri), ((Willemia_trilobata
 1506 , Willemia_namibiae), ((Willemia_similis, (Willemia_christianseni
 1507 , (Willemia_anophthalma, ((Willemia_scandinavica, Willemia_koreana)
 1508 , (Willemia_dubia, (Willemia_virae, ((Willemia_iztaccihuatlensis
 1509 , Willemia_bedosae), (Willemia_tali, (Willemia_unispina, Willemia_psammophi
 1510 la))))
 1511)))), (Willemia_intermedia, (Willemia_shanghaiensis, (Willemia_granulata
 1512 , ((Willemia_fjellbergi, (Willemia_arida, (Willemia_trisphaerae
 1513 , (Willemia_elisabethum, Willemia_denisi))), (Willemia_japonica
 1514 , (Willemia_subbulbosa, ((Willemia_persimilis, Willemia_acantha)
 1515 , (Willemia_bulbosa, (Willemia_meybholae, Willemia_arenicola)))
 1516 , ((Willemia_nepalensis, (Willemia_neocaledonica, (Willemia_nadchatrami
 1517 , Willemia_brevispina))), (Willemia_annapurna, (Willemia_buddenbrocki
 1518 , (Willemia_wandae, (Willemia_nosyboraha, (Willemia_delamarei
 1519 , (Willemia_setonychia, Willemia_deharvengi))))))))) [154.];
 1520 (Hypogastrura_vernalis, (Orogastrura_dilatata, (Xenyllogastrura_octoculat
 1521 a
 1522 , ((Willemia_multilobata, Willemia_bellingeri), ((Willemia_trilobata
 1523 , Willemia_namibiae), ((Willemia_similis, (Willemia_christianseni
 1524 , (Willemia_anophthalma, (Willemia_dubia, ((Willemia_scandinavica
 1525 , Willemia_koreana), ((Willemia_iztaccihuatlensis, Willemia_bedosae)
 1526 , (Willemia_virae, (Willemia_tali, (Willemia_unispina, Willemia_psammophila
 1527)))))
 1528))), (Willemia_intermedia, (Willemia_shanghaiensis, (Willemia_granulata
 1529 , ((Willemia_fjellbergi, (Willemia_arida, (Willemia_trisphaerae
 1530 , (Willemia_elisabethum, Willemia_denisi))), (Willemia_japonica
 1531 , (Willemia_subbulbosa, ((Willemia_persimilis, Willemia_acantha)
 1532 , (Willemia_bulbosa, (Willemia_meybholae, Willemia_arenicola)))
 1533 , ((Willemia_nepalensis, ((Willemia_nosyboraha, Willemia_delamarei)
 1534 , (Willemia_setonychia, Willemia_deharvengi))), (Willemia_annapurna
 1535 , (Willemia_buddenbrocki, (Willemia_wandae, (Willemia_neocaledonica
 1536 , (Willemia_nadchatrami, Willemia_brevispina))))))))) [154.];
 1537
 1538
 1539
 1540

```

1541 will_results.ss is the data matrix with the resulting optimal trees readable by Winclada (obtained by
1542 the will_results.sh script run in POY):

1543 xread 'Generated by POY 4.0' 52 45
1544 Willemia_wandae 1003003111113111112100133111000110111111111111111101
1545 Willemia_virae 100000011000101101010001110100011011110011?000100001
1546 Willemia_trisphaerae
1547 1311221110010011?10100011101000110000110110101100011
1548 Willemia_trilobata 0000000110011011010?1002310000010011010000?1001???01
1549 Willemia_tali 1111?01110001011010100011111000110111100110000110001
1550 Willemia_subbulbosa
1551 1222222111112011010100023101000110010110110100111001
1552 Willemia_similis 1000000110011011010100011101000010010100010000100001
1553 Willemia_shanghaiensis
1554 100022011???????101000??100000110000??011????1??001
1555 Willemia_setonychia
1556 200300311????11101310????11111011011111111????1???11
1557 Willemia_scandinavica
1558 100022011000101101010001110?000110110100010000100001
1559 Willemia_acantha 0300220111?120110121010??101001110111110110100111011
1560 Willemia_bulbosa
1561 0322222111?1201101[01]1010??101001110111110110100111001
1562 Willemia_psammophila
1563 00000001110010110111000331111101000101?01100001?0001
1564 Willemia_persimilis
1565 0300220111?120110121010??101001110111110110100111001
1566 Willemia_nepalensis
1567 1003003111113111012100122111000110111111110111111101
1568 Willemia_neocaledonica
1569 100300311111311111210012210100011011111111111111101
1570 Willemia_namibiae 0000000110011011010?1?02310000010011010000?100100?01
1571 Willemia_nadchatrami
1572 100300311111311111010012210000011011111?0111111??101
1573 Willemia_multilobata
1574 00000201100100??0101000111000000000000000010100100001
1575 Willemia_meybholae 0222222111112111013101023100001111111110110100111011
1576 Willemia_koreana 1000220110001011010100011101000110110100010000100001
1577 Willemia_japonica 1002222110010011010100011101000110010110110100100011
1578 Willemia_iztaccihuatlensis
1579 11000001100010110101000[12][12]1010011101101?01100?0100001
1580 Willemia_intermedia
1581 1300000110010011010100011101000110000110110100100001
1582 Willemia_granulata 1000220110010011010100011101000110000110110100100011
1583 Willemia_unispina 100000001??10011?101000111111101101101001100001??011
1584 Willemia_fjellbergi
1585 133222211001001101010001110100011000011011?1?1100011
1586 Willemia_elisabethum
1587 1111211110010011110101011101001110111110110101100011
1588 Willemia_dubia 1000000110001011010100011101000110110100010000100001
1589 Willemia_denisi 1111111110010011110101011101001110111110110101100011
1590 Willemia_delamarei 100300311????1110121001??11111011011111111????1???01
1591 Willemia_deharvengi
1592 2003003111113111013100123111110110111111110111111111
1593 Willemia_christianseni
1594 1300000110001011010100011101000110010100010000100001
1595 Willemia_buddenbrocki
1596 1003003111113111112100133101000110111111110111111101

```

```

1597 Willemia_brevispina
1598 130320311111311111010012210100011011111111111111101
1599 Willemia_bellingeri
1600 00000201100100110101000111000000000000000010100100001
1601 Willemia_bedosae 1000000110001011010100011101000110110100110000100001
1602 Willemia_arida 1332222110?100110101000??101000110000110110101100011
1603 Willemia_nosyboraha
1604 10030031111?111111100133111110110111111110010????01
1605 Willemia_arenicola 0222222111102111012101023100001111111110110100111001
1606 Willemia_anophthalma
1607 1000000110001011010100011101000100010100010000100001
1608 Willemia_annapurna 1003003111113111013100133101000110111111110111111101
1609 Xenyllogastrura_octoculata
1610 00000001000?010000000101100000000000010010?1000?0000
1611 Orogastrura_dilatata
1612 0000000000000000000000000000000000000101000101000??000
1613 Hypogastrura_vernalis
1614 000000000?0000000000000000000000000000010???000000
1615 ;
1616 cc - 0.51;
1617 ;
1618 proc /;
1619 #
1620 $
1621 ;
1622 cn {0 willemia2011.ss:0 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1623 2 3 4 5 6 7 8 9 ;
1624 {1 willemia2011.ss:1 A B C D E F G H I J K L M N O P Q R S T U V 0 1 2
1625 3 4 5 6 7 8 9 ;
1626 {2 willemia2011.ss:2 A B C D E F G H I J K L M N O P Q R S T U V 0 1 2
1627 3 4 5 6 7 8 9 ;
1628 {3 willemia2011.ss:3 A B C D E F G H I J K L M N O P Q R S T U V 0 1 2
1629 3 4 5 6 7 8 9 ;
1630 {4 willemia2011.ss:4 A B C D E F G H I J K L M N O P Q R S T U V 0 1 2
1631 3 4 5 6 7 8 9 ;
1632 {5 willemia2011.ss:5 A B C D E F G H I J K L M N O P Q R S T U V 0 1 2
1633 3 4 5 6 7 8 9 ;
1634 {6 willemia2011.ss:6 A B C D E F G H I J K L M N O P Q R S T U V 0 1 2
1635 3 4 5 6 7 8 9 ;
1636 {7 willemia2011.ss:7 A B C D E F G H I J K L M N O P Q R S T U V 0 1 2
1637 3 4 5 6 7 8 9 ;
1638 {8 willemia2011.ss:8 A B C D E F G H I J K L M N O P Q R S T U V 0 1 2
1639 3 4 5 6 7 8 9 ;
1640 {9 willemia2011.ss:9 A B C D E F G H I J K L M N O P Q R S T U V 0 1 2
1641 3 4 5 6 7 8 9 ;
1642 {10 willemia2011.ss:10 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1643 2 3 4 5 6 7 8 9 ;
1644 {11 willemia2011.ss:11 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1645 2 3 4 5 6 7 8 9 ;
1646 {12 willemia2011.ss:12 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1647 2 3 4 5 6 7 8 9 ;
1648 {13 willemia2011.ss:13 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1649 2 3 4 5 6 7 8 9 ;
1650 {14 willemia2011.ss:14 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1651 2 3 4 5 6 7 8 9 ;
1652 {15 willemia2011.ss:15 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1653 2 3 4 5 6 7 8 9 ;

```

```

1654 {16 willemia2011.ss:16 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1655 2 3 4 5 6 7 8 9 ;
1656 {17 willemia2011.ss:17 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1657 2 3 4 5 6 7 8 9 ;
1658 {18 willemia2011.ss:18 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1659 2 3 4 5 6 7 8 9 ;
1660 {19 willemia2011.ss:19 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1661 2 3 4 5 6 7 8 9 ;
1662 {20 willemia2011.ss:20 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1663 2 3 4 5 6 7 8 9 ;
1664 {21 willemia2011.ss:21 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1665 2 3 4 5 6 7 8 9 ;
1666 {22 willemia2011.ss:22 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1667 2 3 4 5 6 7 8 9 ;
1668 {23 willemia2011.ss:23 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1669 2 3 4 5 6 7 8 9 ;
1670 {24 willemia2011.ss:24 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1671 2 3 4 5 6 7 8 9 ;
1672 {25 willemia2011.ss:25 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1673 2 3 4 5 6 7 8 9 ;
1674 {26 willemia2011.ss:26 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1675 2 3 4 5 6 7 8 9 ;
1676 {27 willemia2011.ss:27 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1677 2 3 4 5 6 7 8 9 ;
1678 {28 willemia2011.ss:28 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1679 2 3 4 5 6 7 8 9 ;
1680 {29 willemia2011.ss:29 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1681 2 3 4 5 6 7 8 9 ;
1682 {30 willemia2011.ss:30 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1683 2 3 4 5 6 7 8 9 ;
1684 {31 willemia2011.ss:31 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1685 2 3 4 5 6 7 8 9 ;
1686 {32 willemia2011.ss:32 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1687 2 3 4 5 6 7 8 9 ;
1688 {33 willemia2011.ss:33 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1689 2 3 4 5 6 7 8 9 ;
1690 {34 willemia2011.ss:34 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1691 2 3 4 5 6 7 8 9 ;
1692 {35 willemia2011.ss:35 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1693 2 3 4 5 6 7 8 9 ;
1694 {36 willemia2011.ss:36 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1695 2 3 4 5 6 7 8 9 ;
1696 {37 willemia2011.ss:37 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1697 2 3 4 5 6 7 8 9 ;
1698 {38 willemia2011.ss:38 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1699 2 3 4 5 6 7 8 9 ;
1700 {39 willemia2011.ss:39 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1701 2 3 4 5 6 7 8 9 ;
1702 {40 willemia2011.ss:40 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1703 2 3 4 5 6 7 8 9 ;
1704 {41 willemia2011.ss:41 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1705 2 3 4 5 6 7 8 9 ;
1706 {42 willemia2011.ss:42 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1707 2 3 4 5 6 7 8 9 ;
1708 {43 willemia2011.ss:43 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1709 2 3 4 5 6 7 8 9 ;
1710 {44 willemia2011.ss:44 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1711 2 3 4 5 6 7 8 9 ;

```

```

1712 {45 willemia2011.ss:45 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1713 2 3 4 5 6 7 8 9 ;
1714 {46 willemia2011.ss:46 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1715 2 3 4 5 6 7 8 9 ;
1716 {47 willemia2011.ss:47 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1717 2 3 4 5 6 7 8 9 ;
1718 {48 willemia2011.ss:48 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1719 2 3 4 5 6 7 8 9 ;
1720 {49 willemia2011.ss:49 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1721 2 3 4 5 6 7 8 9 ;
1722 {50 willemia2011.ss:50 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1723 2 3 4 5 6 7 8 9 ;
1724 {51 willemia2011.ss:51 A B C D E F G H I J K L M N O P Q R S T U V 0 1
1725 2 3 4 5 6 7 8 9 ;
1726 ;
1727
1728 tread (Hypogastrura_vernalis (Orogastrura_dilatata
1729 (Xenyllogastrura_octoculata ((Willemia_multilobata Willemia_bellingeri)
1730 ((Willemia_trilobata Willemia_namibiae) ((Willemia_similis
1731 ((Willemia_christianseni Willemia_anophthalma) ((Willemia_dubia
1732 (Willemia_scandinavica Willemia_koreana)) (Willemia_iztaccihuatlensis
1733 (Willemia_bedosae ((Willemia_unispina Willemia_psammophila)
1734 (Willemia_virae Willemmai_tali)))))) (Willemia_intermedia
1735 (Willemia_shanghaiensis (Willemia_granulata ((Willemia_fjellbergi
1736 Willemia_arida) (Willemia_trisphaerae (Willemia_elisabethum
1737 Willemia_denisi))) (Willemia_japonica (Willemia_subbulbosa
1738 ((Willemia_persimilis Willemia_acantha) (Willemia_bulbosa
1739 (Willemia_meybholae Willemia_arenicola))) ((Willemia_nepalensis
1740 (Willemia_neocaledonica (Willemia_nadchatrami Willemia_brevispina)))
1741 (Willemia_annapurna (Willemia_buddenbrocki (Willemia_wandae
1742 (Willemia_nosyboraha (Willemia_delamarei (Willemia_setonychia
1743 Willemia_deharvengi)))))))))) * (Hypogastrura_vernalis
1744 (Orogastrura_dilatata (Xenyllogastrura_octoculata
1745 ((Willemia_multilobata Willemia_bellingeri) ((Willemia_trilobata
1746 Willemia_namibiae) ((Willemia_similis ((Willemia_christianseni
1747 Willemia_anophthalma) ((Willemia_dubia (Willemia_scandinavica
1748 Willemia_koreana)) ((Willemia_virae (Willemia_unispina
1749 Willemia_psammophila)) (Willemia_bedosae (Willemia_iztaccihuatlensis
1750 Willemmai_tali)))))) (Willemia_intermedia (Willemia_shanghaiensis
1751 (Willemia_granulata ((Willemia_fjellbergi Willemia_arida)
1752 (Willemia_trisphaerae (Willemia_elisabethum Willemia_denisi)))
1753 (Willemia_japonica (Willemia_subbulbosa ((Willemia_persimilis
1754 Willemia_acantha) (Willemia_bulbosa (Willemia_meybholae
1755 Willemia_arenicola))) ((Willemia_nepalensis (Willemia_neocaledonica
1756 (Willemia_nadchatrami Willemia_brevispina))) (Willemia_annapurna
1757 (Willemia_buddenbrocki (Willemia_wandae (Willemia_nosyboraha
1758 (Willemia_delamarei (Willemia_setonychia
1759 Willemia_deharvengi)))))))))) * (Hypogastrura_vernalis
1760 (Orogastrura_dilatata (Xenyllogastrura_octoculata
1761 ((Willemia_multilobata Willemia_bellingeri) ((Willemia_trilobata
1762 Willemia_namibiae) ((Willemia_similis (Willemia_christianseni
1763 (Willemia_anophthalma (Willemia_dubia ((Willemia_scandinavica
1764 Willemia_koreana) ((Willemia_unispina Willemia_psammophila)
1765 (Willemia_bedosae (Willemia_iztaccihuatlensis (Willemia_virae
1766 Willemmai_tali)))))) (Willemia_intermedia (Willemia_shanghaiensis
1767 (Willemia_granulata ((Willemia_fjellbergi (Willemia_arida
1768 (Willemia_trisphaerae (Willemia_elisabethum Willemia_denisi))))
1769 (Willemia_japonica (Willemia_subbulbosa ((Willemia_persimilis

```

1770 Willemia_acantha) (Willemia_bulbosa (Willemia_meybholae
 1771 Willemia_arenicola))) ((Willemia_nepalensis ((Willemia_nosyboraha
 1772 Willemia_delamarei) (Willemia_setonychia Willemia_deharvengi)))
 1773 (Willemia_annapurna (Willemia_buddenbrocki (Willemia_wandae
 1774 (Willemia_neocaledonica (Willemia_nadchatrami
 1775 Willemia_brevispina))))))))) * (Hypogastrura_vernalis
 1776 (Orogastrura_dilatata (Xenyllogastrura_octoculata
 1777 ((Willemia_multilobata Willemia_bellingeri) ((Willemia_trilobata
 1778 Willemia_namibiae) ((Willemia_similis (Willemia_christianseni
 1779 (Willemia_anophthalma ((Willemia_scandinavica Willemia_koreana)
 1780 (Willemia_dubia ((Willemia_unispina Willemia_psammophila)
 1781 (Willemia_virae (Willemia_bedosae (Willemia_iztaccihuatlensis
 1782 Willemia_tali))))))))) (Willemia_intermedia (Willemia_shanghaiensis
 1783 (Willemia_granulata (((Willemia_fjellbergi Willemia_arida)
 1784 (Willemia_trisphaerae (Willemia_elisabethum Willemia_denisi)))
 1785 (Willemia_japonica (Willemia_subbulbosa (((Willemia_persimilis
 1786 Willemia_acantha) (Willemia_bulbosa (Willemia_meybholae
 1787 Willemia_arenicola))) ((Willemia_nepalensis ((Willemia_nosyboraha
 1788 Willemia_delamarei) (Willemia_setonychia Willemia_deharvengi)))
 1789 (Willemia_annapurna (Willemia_buddenbrocki (Willemia_wandae
 1790 (Willemia_neocaledonica (Willemia_nadchatrami
 1791 Willemia_brevispina))))))))) * (Hypogastrura_vernalis
 1792 (Orogastrura_dilatata (Xenyllogastrura_octoculata
 1793 ((Willemia_multilobata Willemia_bellingeri) ((Willemia_trilobata
 1794 Willemia_namibiae) ((Willemia_similis (Willemia_christianseni
 1795 (Willemia_anophthalma ((Willemia_scandinavica Willemia_koreana)
 1796 (Willemia_dubia (Willemia_virae ((Willemia_iztaccihuatlensis
 1797 Willemia_bedosae) (Willemia_tali (Willemia_unispina
 1798 Willemia_psammophila))))))))) (Willemia_intermedia
 1799 (Willemia_shanghaiensis (Willemia_granulata ((Willemia_fjellbergi
 1800 (Willemia_arida (Willemia_trisphaerae (Willemia_elisabethum
 1801 Willemia_denisi))) (Willemia_japonica (Willemia_subbulbosa
 1802 (((Willemia_persimilis Willemia_acantha) (Willemia_bulbosa
 1803 (Willemia_meybholae Willemia_arenicola))) ((Willemia_nepalensis
 1804 (Willemia_neocaledonica (Willemia_nadchatrami Willemia_brevispina)))
 1805 (Willemia_annapurna (Willemia_buddenbrocki (Willemia_wandae
 1806 (Willemia_nosyboraha (Willemia_delamarei (Willemia_setonychia
 1807 Willemia_deharvengi))))))))) * (Hypogastrura_vernalis
 1808 (Orogastrura_dilatata (Xenyllogastrura_octoculata
 1809 ((Willemia_multilobata Willemia_bellingeri) ((Willemia_trilobata
 1810 Willemia_namibiae) ((Willemia_similis (Willemia_christianseni
 1811 (Willemia_anophthalma (Willemia_dubia ((Willemia_scandinavica
 1812 Willemia_koreana) ((Willemia_iztaccihuatlensis Willemia_bedosae)
 1813 (Willemia_virae (Willemia_tali (Willemia_unispina
 1814 Willemia_psammophila))))))))) (Willemia_intermedia
 1815 (Willemia_shanghaiensis (Willemia_granulata ((Willemia_fjellbergi
 1816 (Willemia_arida (Willemia_trisphaerae (Willemia_elisabethum
 1817 Willemia_denisi))) (Willemia_japonica (Willemia_subbulbosa
 1818 (((Willemia_persimilis Willemia_acantha) (Willemia_bulbosa
 1819 (Willemia_meybholae Willemia_arenicola))) ((Willemia_nepalensis
 1820 ((Willemia_nosyboraha Willemia_delamarei) (Willemia_setonychia
 1821 Willemia_deharvengi))) (Willemia_annapurna (Willemia_buddenbrocki
 1822 (Willemia_wandae (Willemia_neocaledonica (Willemia_nadchatrami
 1823 Willemia_brevispina)))))))))
 1824
 1825

1826 bremer_w.sh and jackknife_w.sh are the scripts for bremer and jackknife calculation respectively; will-
 1827 one.tre file contains one of the six optimal tree for the purpose of these calculations;

1828

1829 bremer_w.sh:

```
1830 wipe ()
1831 read ("willemia2011.ss")
1832 set (root: "Hypogastrura_venalis")
1833 read ("willone.tre")
1834 report ("bremerw.txt", supports:bremer:"will-brel.trees")
1835 report ("bremerw", graphsupports:bremer:"will-brel.trees")
1836 exit ()
```

1837

1838

1839 jackknife_w.sh:

```
1840 wipe ()
1841 read ("willemia2011.ss")
1842 set (root: "Hypogastrura_venalis")
1843 read ("will-one.tre")
1844 calculate_support(jackknife:(remove:0.50, resample:1000), build(),
1845 swap(tbr, trees:5))
1846 report ("jackknife_w", graphsupports:jackknife)
1847 exit ()
```

1848

1849

1850 will-one.tre:

```
1851 (Hypogastrura_venalis, (Orogastrura_dilatata, (Xenyllogastrura_octoculata
1852 a
1853 , ((Willemia_multilobata, Willemia_bellingeri), (Willemia_trilobata
1854 , Willemia_namibiae), ((Willemia_similis, (Willemia_christianseni
1855 , Willemia_anophthalma), ((Willemia_dubia, (Willemia_scandinavica
1856 , Willemia_koreana)), (Willemia_iztaccihuatlensis, (Willemia_bedosae
1857 , ((Willemia_unispina, Willemia_psammophila), (Willemia_virae, Willemia_tal
1858 i))))))
1859 ), (Willemia_intermedia, (Willemia_shanghaiensis, (Willemia_granulata
1860 , ((Willemia_fjellbergi, Willemia_arida), (Willemia_trisphaerae
1861 , (Willemia_elisabethum, Willemia_denisi))), (Willemia_japonica
1862 , (Willemia_subbulbosa, ((Willemia_persimilis, Willemia_acantha)
1863 , (Willemia_bulbosa, (Willemia_meybholae, Willemia_arenicola)))
1864 , ((Willemia_nepalensis, (Willemia_neocaledonica, (Willemia_nadchatrami
1865 , Willemia_brevispina))), (Willemia_annapurna, (Willemia_buddenbrocki
1866 , (Willemia_wandae, (Willemia_nosyboraha, (Willemia_delamarei
1867 , (Willemia_setonychia, Willemia_deharvengi)))))))))) [154.];
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Appendix S1d: Willemia phylogeny and characters: results

Figure Appendix S1 shows the strict consensus of 6 most parsimonious trees with a tree length of 154 steps, with jackknife and Bremer indices indicated at each node. Consistency Index is 46 and Retention Index is 82. All trees, jackknife, statistics and Bremer supports can be found in Electronic Appendix S1c. The addition of the 5 new *Willemia* species did not change the general topology found in D'Haese (2000). The monophyly of the genus *Willemia* was confirmed and strongly supported (jackknife resampling percentage of 100% and Bremer support value 3). The *anophthalma*, *denisi* s.str. and *buddenbrocki* groups were retrieved monophyletic again and the *denisi* group *sensu* Potapov is still paraphyletic (with the addition of *W. shanghaiensis* between *W. intermedia* and *W. granulata* in a paraphyletic assemblage). The new species (for the analysis) *W. tali*, *W. iztacihuatlensis*, *W. psammophila* and *W. unispina* belong to the *anophthalma* group. *W. acantha* is sister group to *W. persimilis*, in the same group, *W. bulbosa* is sister group to *W. arenicola* + *W. meybholae*. Lastly, *W. nosyboraha* is included in the *buddenbrocki* group. Table 1 and Table in Appendix S2e show biogeographic and ecological attributes of species, respectively. In these tables species were arranged in the order given by the phylogeny.

1887

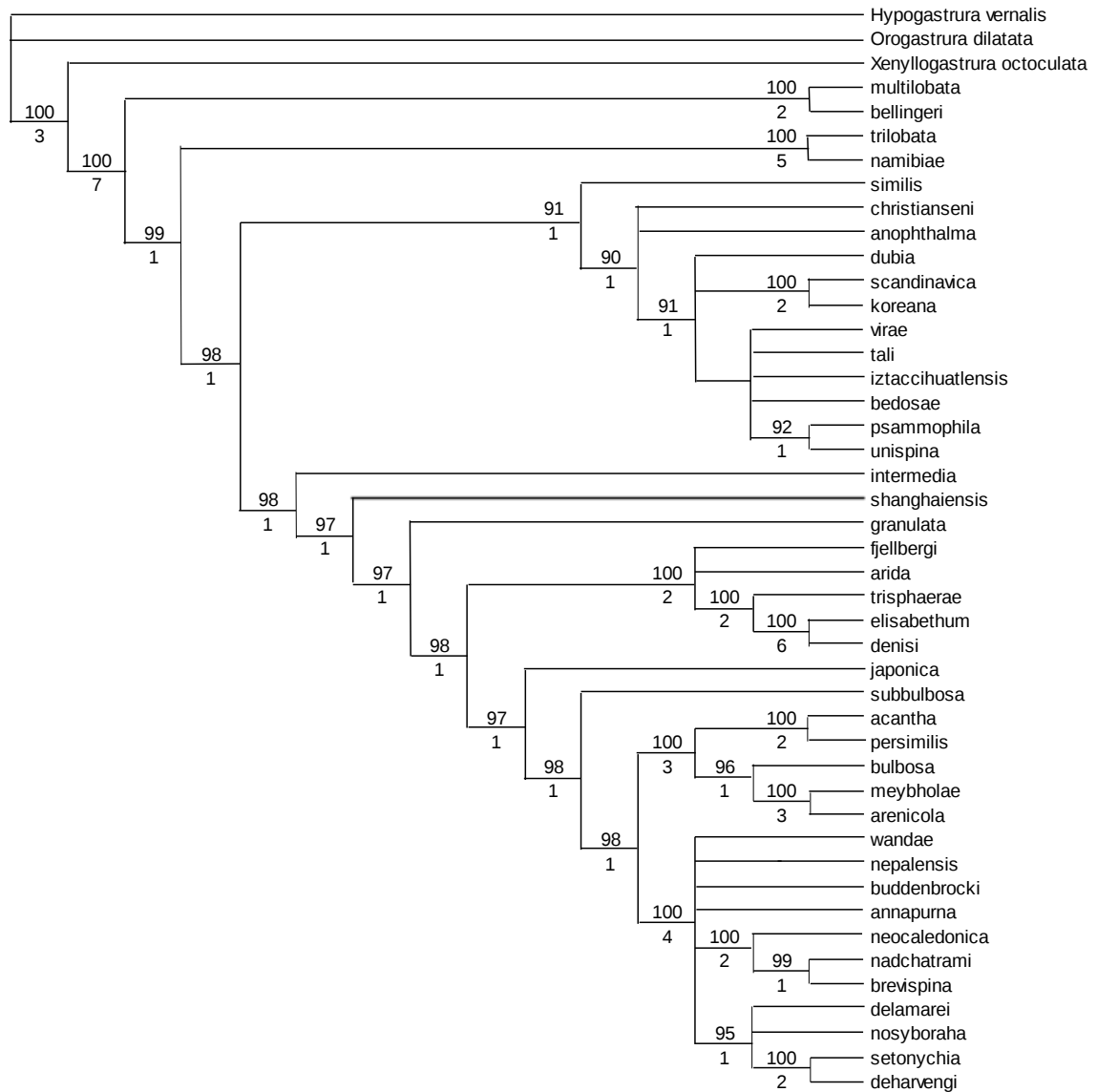
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Figure Appendix S1. Strict majority consensus of six phylogenetic trees of the genus *Willemia*, with three outgroup species (see text for more details). Jackknife resampling percentages and Bremer support values are indicated above and below each node, respectively.



1899 **Appendix S2: Literature research: definitions, references, exploration of biases**

1900 Appendix S2a – Definitions of factors of harshness

- 1901 - ‘xeric’ was defined as an environment displaying permanent or seasonal aridity: deserts
 1902 (whether warm or cold), matorrals, sand dunes with poor vegetation cover, karst landscapes
 1903 and dry Mediterranean areas
- 1904 - ‘hydric’ was defined as an environment displaying excess of water and associated lack of
 1905 soil atmosphere: waterlogged soils, flooded areas
- 1906 - ‘arctic’ was defined as an environment displaying a long period of frost, generally more than
 1907 six months, reflecting a latitudinal temperature gradient: polar, arctic and subarctic
 1908 environments
- 1909 - ‘alpine’ was defined as an environment displaying a long period of frost, generally more
 1910 than six months, reflecting an altitudinal temperature gradients: high mountains, including
 1911 alpine and subalpine climates, above 1,000 m in nordic countries, above 2,000 m in temperate
 1912 areas, above 3,000 or 4,000 m in tropical areas
- 1913 - ‘acid’ was defined as a soil at pH_{water} less than 5, where free aluminium and high phenolic
 1914 concentrations are likely to occur: raw humus, podzols
- 1915 - ‘metallic’ was defined as a soil polluted with heavy metals: areas in the vicinity of smelter or
 1916 mining activities
- 1917 - ‘saline’ was defined as a soil with a high osmotic pressure due to a high charge in salts
 1918 (beaches and salt deserts).
- 1919 Every species could be assigned to several harsh habitats according to (i) multiple records of
 1920 the same species in a variety of habitats, or (ii) habitats belonging to several harshness

categories. For instance, over the whole array of literature consulted, the same species can be recorded both in waterlogged and arid soils or the same habitat can be ‘arctic’ and ‘acid’, but only when this was indicated. In our census we did not try to discern whether some factors were dominant above others in a given record unit. Rather we considered them as independent causes of harshness, with which species must cope within a given habitat throughout their evolutionary history (Jablonski, 2008).

Caves were excluded given that (i) they constitute refuges where more sensitive species can live in a more buffered environment, whatever the nature of the surrounding environment, (ii) there was no evidence they were detrimental to growth and reproduction of most soil invertebrate species (Moseley, 2007), and (iii) some *Willemia* species were reported to occur in caves (some of them were even described for the first time in caves) but they were also found in other environments, suggesting the absence of specialisation for cave life in this genus (Christiansen, 1965). Psammophily sensu D’Haese (2000), i.e. life in sand, was partitioned in ‘saline’ and ‘xeric’ categories according to whether sea water or drought was the prevailing factor. For instance seashore dunes were considered ‘xeric’ but not ‘saline’ while the intertidal zone was considered ‘saline’ but not ‘xeric’. Experimental studies focusing on individual *Willemia* species as well as on entire soil communities were also taken into account. The ‘harshness breadth’ index was estimated for every species by the number of harsh environments in which the species was recorded, thus scaling from 0 (no harsh environment recorded for the species) to 7 (all harsh environments recorded).

Obviously, no place on earth will show all types of harshness. This is why we considered multiple types of harshness, and why we quantified the harshness breadth as the number of harshness types occupied by a given species. Moreover, we tested whether occupation of different types of harshness is positively or negatively correlated, i.e. whether species that can tolerate certain kinds of harsh environments tend to be able to tolerate a broad

1946 range of harsh environments (except those affected by salinity). We found that occupations of
 1947 all but one type of harshness are positively correlated (Results). This means that a species that
 1948 is found in environments that are harsh in one type tend to be found under different types of
 1949 harsh environments, too. Inversely, other species occupy environments lacking any of the
 1950 types of harshness. This result justifies talking broadly about “species using harsh
 1951 environments” as we repeatedly do it.

1952 The largest possible corpus of literature was examined for the assessment of use of
 1953 harsh environments in *Willemia* species. As defined above (Introduction), harsh environments
 1954 are those which limit the rate of growth and reproduction of most species, except a few ones
 1955 tolerating it. This does not mean that harsh environments are poorer in Collembolan
 1956 individuals, since better adapted species may benefit from the alleviation of competition
 1957 caused by the resulting decrease in species richness and thereby may locally proliferate
 1958 (Usher, 1985). A total of 248 references were used for the census (Appendix S2b). Languages
 1959 available to us were English, French, German, Italian, Portugese and Spanish, embracing most
 1960 literature published in books and scientific journals. Other languages (Russian, Japanese,
 1961 Hungarian) were cautiously discarded, in order to avoid misinterpretation, but they comprised
 1962 less than 1% of published literature. When information about soil or climate was not given for
 1963 a record, but the plant community was sufficiently described in the vicinity of the sample,
 1964 then vegetation was used as a basis for estimating the harshness of the environment: in several
 1965 instances dominant ericaceous or coniferous vegetation was considered as indicative of soil
 1966 acidity given the recalcitrance of its litter and its known acidifying influence on the
 1967 environment occupied by *Willemia* (Ponge, 2000), while grassland species were indicative of
 1968 more fertile and less acid soils (Miles, 1985; Falkengren-Grerup, 1986). In two instances, the
 1969 geographic locality was sufficiently precise and was used to derive environmental conditions

1970 prevailing at the sampling site. In the absence of any clue on environmental conditions,
 1971 records were disregarded.

1972 The above classification might miss species that are able to use harsh environments
 1973 but did not happen to encounter any. However, given that we accounted for a large range of
 1974 harsh environments, species in all regions should have encountered at least some of them (and
 1975 use of one kind of harsh environment turn out to be positively correlated to the use of all
 1976 others in most cases, see Results). Not occurring in harsh environments is hence true evidence
 1977 for not being able to use them.

1978

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- 1998

1999 Appendix S2b - References used for the assessment of use of harsh environments in *Willemia*

2000 species.

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[illegible]

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dubia	3	Weiner (1986)
elisabethum	1	Babenko (2003a, b), Thibaud (2004)
fjellbergi	3	Fjellberg (1984, 1985), Addison et al. (2006)
granulata	3	Mills (1934), Bellinger (1954), Hüther (1962), Wray et al. (1963), Szeptycki (1967), Gough (1972), Huhta et al. (1979), Lienhard (1980), Ponge & Prat (1982), Ponge (1983), Arpin et al. (1984), Ponge (1984), Arbea & Jordana (1986), Bolger (1986), Weiner (1986), Lucíañez Sánchez & Simón Benito (1988), Simón Benito & Pozo Martínez (1988), Fjellberg (1988), Sterzynska (1989), Arbea & Jordana (1990), Rusek (1990), Zerling (1990), Sterzinska (1990), Palacios-Vargas (1990), Fjellberg (1992), Ponge (1992), Battigelli & Marshall (1993), Kováč & Miklisová (1995), Rusek & Marshall (1995), Filser (1995), Ponge (1997), Jordana et al. (1997), da Gama et al. (1997, 1998), Fjellberg (1998), Barrocas et al. (1999), Ponge (2000a), Loranger et al. (2001), Otrysko & Pagé (2001), Shrubovych (2002), Traser (2002), Stebaeva (2003), Addison et al. (2003), Ponge et al. (2003), Petersen et al. (2004), Dunger et al. (2004), Kováč et al. (2005), Gillet & Ponge (2005), Traser & Horváth-Szováti (2006), Addison et al. (2006), Sleptzova & Reznikova (2006), Debeljak et al. (2007), Hopkin (2007), Raschmanová et al. (2008)
intermedia	60	García-Gómez & Cutz-Pool (2008), García-Gómez et al. (2009)
iztacchuatlen	2	Tanaka & Kitazawa (1982), Thibaud (2004)
sis		Thibaud & Lee (1994), Thibaud (2004)
japonica	2	Palacios-Vargas (1987)
koreana	2	Gers & Deharveng (1985), Fjellberg (1992, 1998), Babenko (2003a, b), Sterzynska & Bolger (2004), Hopkin (2007)
meybholae	1	Yosii (1959), McClure et al. (1967)
multilobata	8	Thibaud & Massoud (1988)
nadchatrami	2	Weiner (1991), d'Haese & Weiner (1998), Thibaud (2002, 2009a, b)
namibiae	1	d'Haese & Weiner (1998), Thibaud (2004)
neocaledonica	5	Thibaud (2008)
nepalensis	2	Bonet (1945), Hüther (1962), Palacios-Vargas (1981), Palacios-Vargas & Gómez-Anaya (1993), Palacios-Vargas (2004), Cutz-Pool et al. (2007)
nosyboraha	1	Palacios-Vargas & Thibaud (2001)
persimilis	6	Gisin (1947), Haybach (1959), Hüther (1962), Gough (1972), Dunger (1975), Fjellberg (1976, 1977), & Jordana (1986), Fjellberg (1988, 1994), Babenko (1994), Hertzberg et al. (1994), Kováč (1994), Marshall (1995), Koehler et al. (1995), Sterzyńska & Ehrnsberger (1997), Jordana et al. (1997), Traser (1999), Babenko (2000), Shrubovych (2002), Traser (2002), Bondarenko-Borisova & Saratovskaya (2003), Babenko (2003a, b), Thibaud (2004), Kováč et al. (2005), Sørensen et al. (2006), Traser & Horváth-Szováti (2006), Arbea & Martínez Monteagudo (2006), Moseley (2007), Hopkin (2007), Raschmanová et al. (2008)
psammophila	1	Prabhoo (1971)
scandinavica	34	Yue (1999)
setonychia	1	Mills (1934), Weber (1950), Wray (1950), Wray et al. (1963), Benner & Kannowski (1984), Fjellberg (1986, 1988), Rusek (1994), Babenko (1994), Fjellberg (1994, 1998), d'Haese (1998), Babenko (1999), Thibaud (2004), Sørensen et al. (2006), Addison et al. (2006)
shanghaiensis	1	Thibaud (1994)
similis	20	Kaprus' & Nevo (2003)
subbulbosa	1	Barra (1995)
tali	1	Babenko (2002), Stebaeva (2003), Babenko (2003a, b), Thibaud (2004), Babenko (2008, 2009)
trilobata	1	Fjellberg (2007)
trisphaerae	7	Kaprus' (1997), Skarżyński & Smolis (2002), Thibaud (2004), Traser & Horváth-Szováti (2006), (2006)
unispina	1	Tamura & Zhao (1997), d'Haese & Weiner (1998), Thibaud (2004)
virae	5	
wandae	3	

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2592 Appendix S2c – Exploration of bias due to differences between species in numbers of records
2593 in the literature.

2594

2595 Methods: Because species differed in the number of records from which harshness-breadth
2596 was estimated (see above Appendix S2b, column 2), we also verified whether the number of
2597 records was ‘phylogenetically conserved’. For this, we also used the root-skewness test with
2598 Euclidean distances among species. This test aims to highlight whether our results were
2599 biased by differences among species in the amount of knowledge on their environmental
2600 distribution. This approach is conservative: the intensive study of a species may increase the
2601 number of records in harsh environments (bias), but a species’ use of harsh environments may
2602 also increase the chance of being observed in many of the environments studied (non-bias).

2603

2604 Results: There was no phylogenetic structure in the number of literature records (root-
2605 skewness test P-value = 0.326) even after log-transformation (root-skewness test P-value =
2606 0.291) indicating that the analyses done in the main text on the link between phylogeny and
2607 properties of species do not depend on the extent to which these species were studied in the
2608 literature.

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2612 Appendix S2d: Salinity and tolerance to harshness.

2613 We showed that in the genus *Willemia* tolerance to salinity (use of haline habitats) was negatively
 2614 correlated to other types of harshness and that ‘haline’ species exhibited on average a higher clade
 2615 rank than species tolerant of other harshness factors such as drought, frost, acidity, waterlogging
 2616 (anaerobiosis) or heavy metals. In the absence of ecophysiological studies on the genus *Willemia*,
 2617 which is probably explained by the small size of these animals and their concealed way of life
 2618 (d’Haese, 2000), only putative arguments can be given for rejecting salinity as a harshness factor to
 2619 which *Willemia* should adapt for life on the seashore. A strong attraction to sodium (compared to
 2620 potassium) has been shown to occur in *Heteromurus nitidus*, another soil-dwelling springtail species
 2621 (Salmon et al., 2002). Thibaud (2007), on the base of biogeographic arguments, postulated that
 2622 transport by sea currents could be responsible for the occurrence of the same *Willemia* species on
 2623 remote seashores, whether insular or continental. Witteveen *et al.* (1987) showed that the ionic
 2624 concentration of the haemolymph of inland Collembola equilibrated rapidly with sea water when
 2625 transferred to seashore conditions. It could be suggested that permanent contact with dilute saline
 2626 solutions (seashores, but not dry saline environments) needs no special adaptation in basal Hexapoda,
 2627 contrary to fully terrestrial insects (higher insects), for which potassium is an essential element which
 2628 replaces sodium (Wigglesworth, 1965). The ancestry of life in sea water versus freshwater has been
 2629 shown to be the rule in aquatic invertebrates (Lee & Bell, 1999). The separation we performed
 2630 between tolerance to drought and to salinity, based on ecophysiological and biocenotic grounds
 2631 (Hartmut *et al.*, 1995; Thibaud, 2007), and supported by studies on other animal groups (Gomez-
 2632 Mestre & Tejedo, 2005), might explain why psammophily (life in sand), which confounds both
 2633 adaptation to drought and to salinity, exhibits a high degree of reversal along phylogenetic trees of the
 2634 genus *Willemia* (d’Haese, 2000).

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2661 Appendix S2e: Identification and interpretation of biogeographic provinces.

2662

2663 The Gondwana (Antarctica, South America, Africa, Australasia, Madagascar, India and
 2664 Himalaya, South-East Asia, Caribbean) or Laurasia (North America, Greenland, Europe, Asia
 2665 except South-East Asia) origin of each biogeographic province was estimated from maps by
 2666 McLoughlin (2001), except for Macaronesia (volcanic islands of North Atlantic) and Central
 2667 America which did not exist at the time of Pangea disruption and the spread of present-day
 2668 continents. Obviously, these two biogeographic distributions are strongly linked but they are
 2669 not identical. While all 20 species from the former Laurasia domain are extra-tropical, only 8
 2670 of the 12 species from former Gondwana domain are tropical. In the latter analyses we only
 2671 accounted for the 32 species which could be classified for both tropical/non-tropical and
 2672 Gondwana/Laurasia distribution, permitting better comparability. Accounting for all species,
 2673 however, lead to the same qualitative conclusions. We are aware of the fact that strong
 2674 geographic discrepancies exist in the sampling effort devoted to Collembola (Deharveng,
 2675 2004). This is why we used the number of records per species (used as a proxy for sampling
 2676 effort) to check for the absence of biases due to sampling imbalances (see Appendix S2c).

2677 The above biogeographic classifications correspond to very general trends in
 2678 environmental harshness. For species that are particularly sensitive to moisture deficits, such
 2679 as the majority of Collembola, regions receiving a high amount of rainfall will on average be
 2680 less harsh. For species that are not able to increase their body temperature above that of the
 2681 immediate environment, such as again Collembola, regions of high temperatures will on
 2682 average be less harsh. In that sense, the Inter-Tropical Convergence Zone, with a reasonably
 2683 warm (cloudy) and moist climate, will be favorable to most sensitive species. Besides
 2684 coldness and aridity, acid and metal-contaminated soils were also considered as harsh

habitats. Indeed, most tropical soils are acid, at least they exhibit pH values less than 5. However, if we except areas degraded by human activities in the tropics (pasture, mining,...), tropical rain forests are not characterized by nutrient shortage, due to (i) high organic inputs from the overstory, (ii) a high rate of mineral weathering in the soil. Tropical soils are fragile but not poor in nutrients, at least in the top few centimeters where most soil animals (*Willemia* included) are living (see Dos Santos Neves *et al.*, 2010; Brookshire *et al.*, 2012). Obviously, tropical areas also include harsher environments (which have been coded as such in our database), more especially in mountains above 3000 m (the Andes), white sands and seashores. As explained in the Introduction, during much of the geological past, environments might have been on average harsher on Laurasia rather than on Gondwana paleocontinents (Vršanský, 2005; Crisp *et al.*, 2010), among others reflecting the larger surface of landmasses of northern than of southern temperate regions which may lead to more climatic and thereby edaphic extremes in Laurasia and descendant land masses (except for Antarctica) (Chown *et al.*, 2004).

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- 2718
- 2719

Appendix 3 – Table. Biogeographic provenance of *Willemia* species. Biogeographic provinces according to Christiansen & Bellinger (1995). Gondwana-inherited province in italic type, Eurasia-inherited provinces in italic type, non-defined (Macaronesia and Central America) in normal type. Species belonging to both old continents were classified as Palearctica. Columns corresponding to tropical provinces are shaded

[illegible]

[illegible]

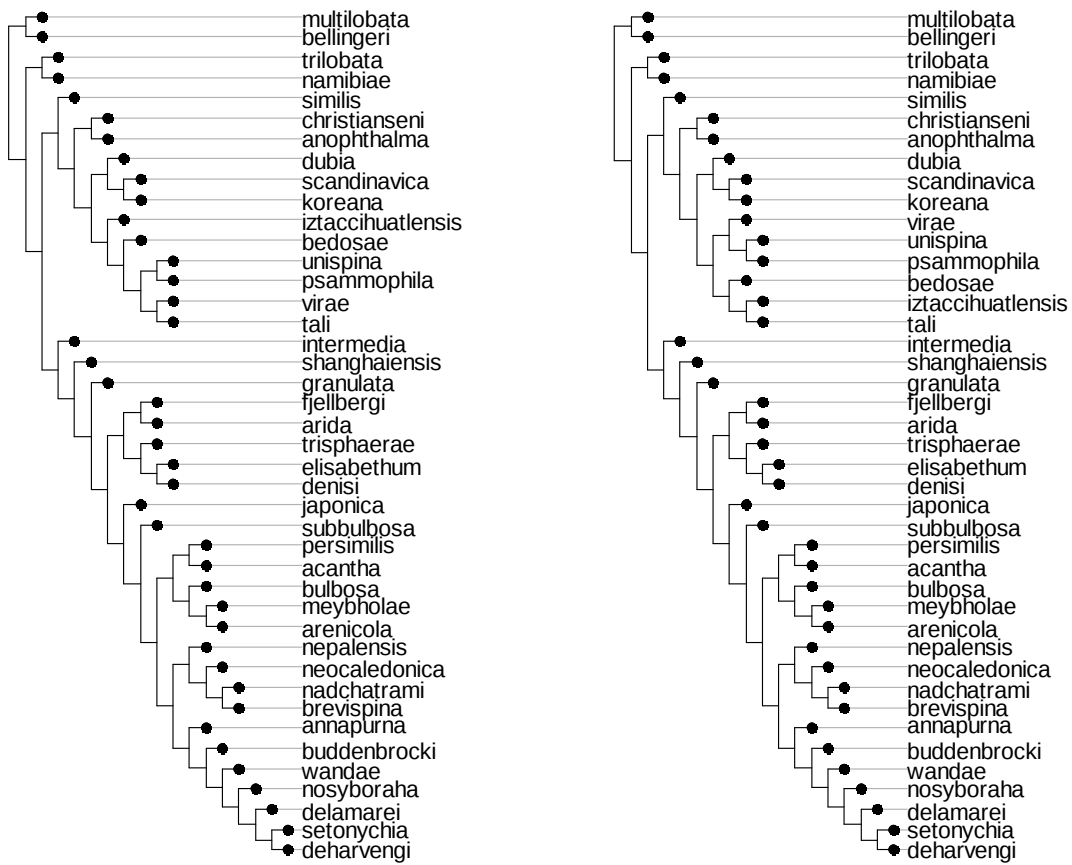
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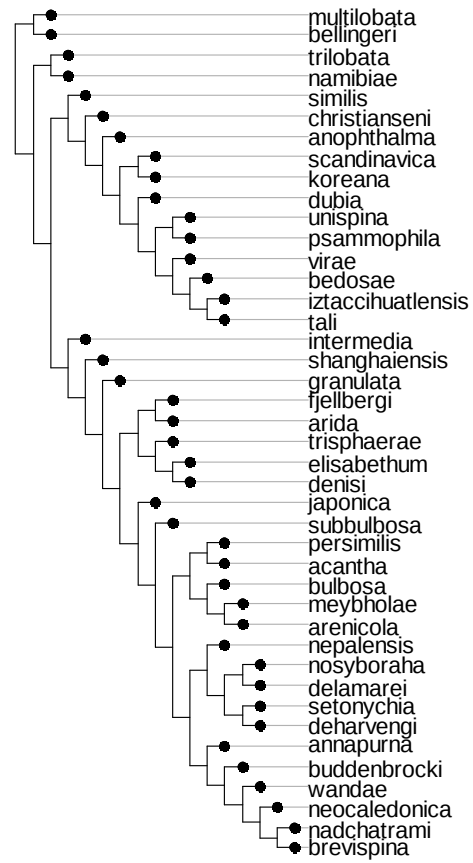
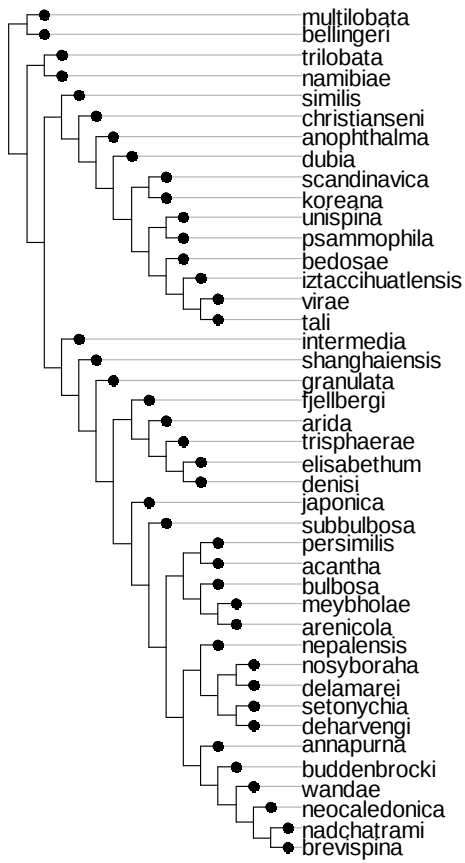
2722 **Appendix S3. Robustness of the analysis to variation in underlying phylogenetic trees**

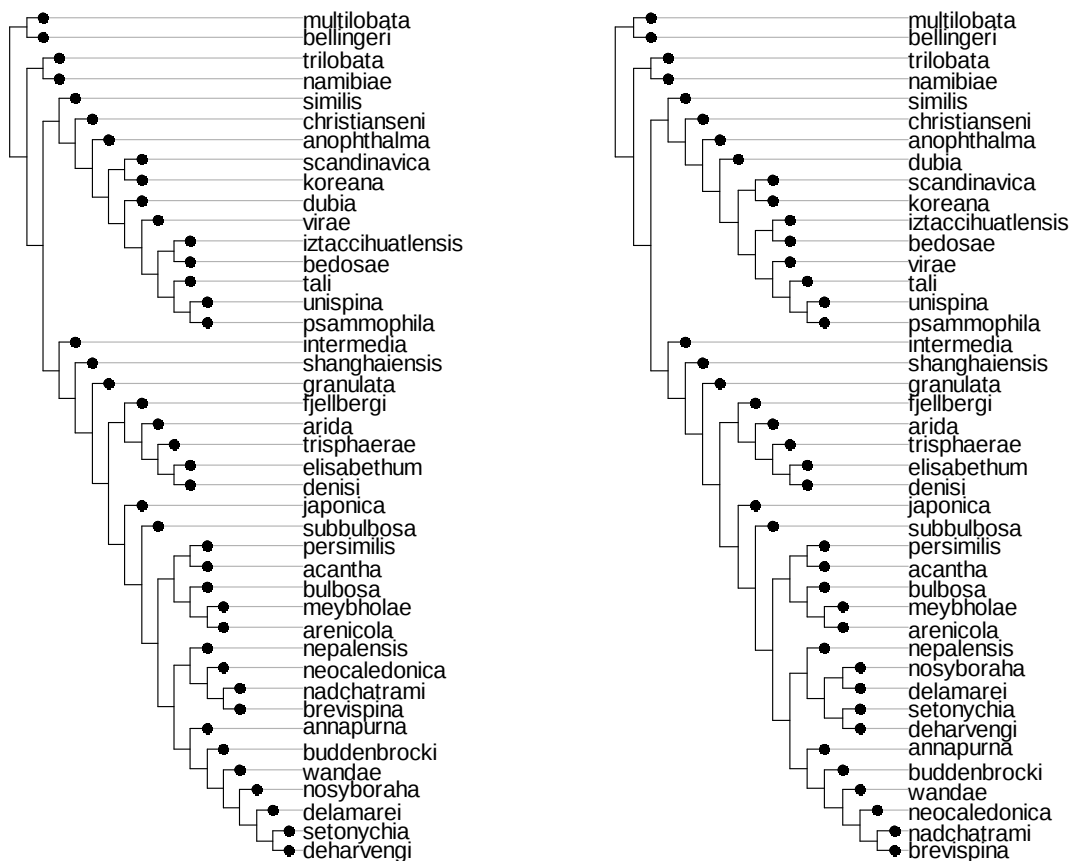
2723 We have performed again all analyses with the 6 most parsimonious trees. The 6 trees are
 2724 given below.

2725 *According to all these analyses, the results obtained with the 6 most parsimonious trees are*
 2726 *equivalent to those obtained with the resulting tree used in the main text.*



2727





2729

2730

2731

2732 **Phylogenetic conservatism in the use of harsh habitats**

2733 With all phylogenetic trees, the types of harshness under which species were found exhibited

2734 clear phylogenetic conservatism (root-skewness test P values varied from 0.001 to 0.003 for a

2735 statistic varying from 0.616 to 0.647, 1 meaning that the whole trait variation is at the root

2736 node). Also the number of types of harsh habitats used by a species was phylogenetically

2737 conserved (root-skewness test P values varied from 0.013 to 0.043, for a statistic varying from

2738 0.623 to 0.660). When salinity was excluded from the array of harsh habitats a stronger

2739 conservatism was registered (root-skewness test P values varied from 0.001 to 0.019, for a

2740 statistic varying from 0.659 to 0.699). The presence/absence of *Willemia* species in harsh

2741 habitats (instead of their number used) exhibited an even clearer phylogenetic conservatism

2742 when salinity was excluded from the array of harsh habitat (root-skewness test with all P
2743 values equal to 0.001, for a statistic varying from 0.754 to 0.786).

2744 **Uses of most types of harsh habitats are positively correlated**

2745 Phylogenetic principal components analysis (pPCA) showed strong positive correlations
2746 between all types of harsh habitats, with the exception of salinity. Use of all other types of
2747 harsh habitats scored distinctly positively on the same Principal Component (Fig. 1).

2748

2749 Appendix S3 Table. Ordination of correlations between uses of different types of harsh
 2750 habitats, analysed by pPCA analysis (multivariate analysis based on phylogenetic distances).
 2751 The table gives coordinates of harsh habitat types along the first principal component for the 6
 2752 dichotomous phylogenies provided above. Note that except for salinity, uses of habitats of all
 2753 types of harshness are positively correlated.

	Phy1	Phy2	Phy3	Phy4	Phy5	Phy6
Xeric	-.343	-.398	-.396	-.414	-.426	-.395
Hydric	-.183	-.177	-.190	-.176	-.181	-.188
Arctic	-.389	-.395	-.380	-.420	-.398	-.373
Alpine	-.482	-.453	-.461	-.432	-.450	-.470
Acid	-.581	-.559	-.566	-.548	-.552	-.567
Metallic	-.201	-.198	-.197	-.202	-.190	-.195
Saline	.296	.312	.303	.305	.291	.299

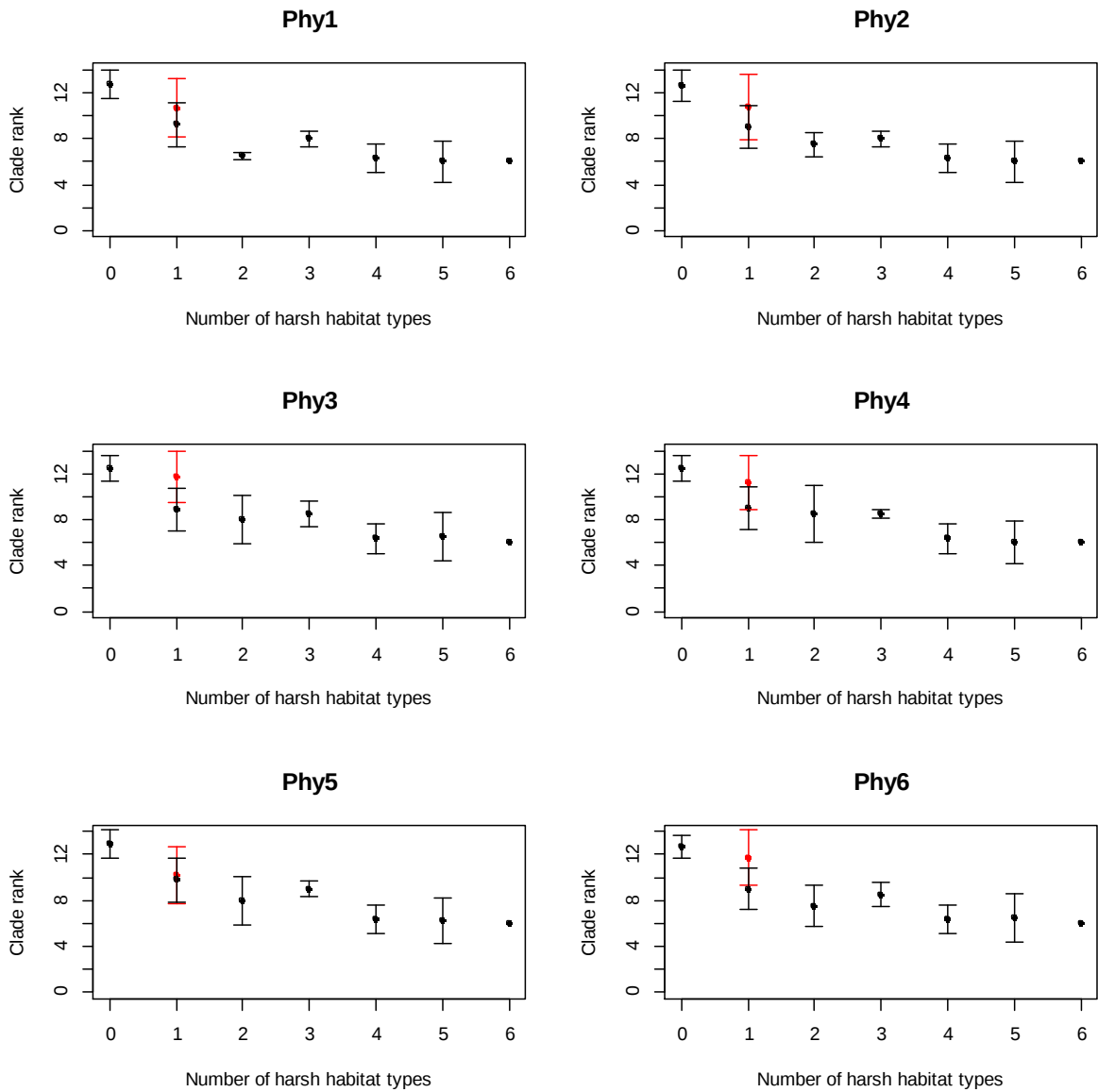
2754

2755

2756 **Species using harsh habitats have lower clade ranks but are as numerous as species**
 2757 **using mesic habitats**

2758 We found that the clade rank of species decreased with species' harshness breadth (PGLS;
 2759 df=40, P values varied from 0.002 to 0.003 depending on the dichotomous phylogeny used).
 2760 When salinity was excluded it appeared that the distance to the root of the phylogenetic tree
 2761 was quite similar for all species using harsh habitats, independent of the number of harsh

2762 habitat types they were using, all of the harshness-tolerant species being placed in a basal
2763 position (Appendix S4 Figure).



2764

2765 **Appendix S3 Figure.** Clade ranks, i.e. nodal distances to the root, of species using different

2766 numbers of harsh habitat types. Error bar = S.E. Note that species that do not use any

2767 harsh habitat are at a higher distance from the root (see text for analyses). This

2768 analysis has been done for each dichotomous phylogenetic tree given above. Species

2769 having a single harsh habitat type have been separated into those affected by salinity

2770 (red) and those affected by another harsh habitat type (black).

2771

2772 **Geographical distributions: Species using harsh habitats tend to be Laurasian, and as a**
 2773 **statistical consequence Laurasians tend to have low clade ranks**

2774 We found that species using harsh and mesic habitats were distributed differently across the
 2775 globe. Species using harsh habitats tended to occur in present non-tropical regions, albeit the
 2776 relationship was relatively weak (PGLS; $df = 30$; P values varying from 0.0004 to 0.0553). At
 2777 the same time, species using harsh habitats were strongly restricted to former Laurasia regions
 2778 (PGLS; $df = 30$; P values varying from 0.0002 to 0.0103).

2779 Low clade-rank species were strongly restricted to present non-tropical regions ($n = 31$
 2780 in all tests of this paragraph, tests based on phylogenetic permutations, all P values equal
 2781 0.001 whatever the dichotomous phylogenetic tree used). This relationship was maintained
 2782 when including harshness breadth as a co-variable: harshness breadth and presence in present-
 2783 day tropical regions were both related to low clade rank (P values were equal to 0.001 for
 2784 harshness breadth, and they varied from 0.001 to 0.009 for presence in present-day tropical
 2785 regions depending on the phylogenetic tree used; conclusions were not impacted by the order
 2786 in which the two explanatory variables were entered in the model: changing the order gave P
 2787 varying from 0.034 to 0.051 for harshness breadth, and equal 0.001 for presence in present-
 2788 day tropical regions). Therefore the high harshness-tolerance of non-tropical species did not
 2789 explain their low clade rank. Species of low clade rank also tended to be restricted to former
 2790 Laurasia regions (P varied from 0.005 to 0.013 depending on the phylogenetic tree used).
 2791 When including first occurrence in former Laurasia and second harshness breadth, both
 2792 variables were significant (P varied from 0.002 to 0.004 for occurrence in former Laurasia,
 2793 and from 0.007 to 0.017 for harshness breadth). But this relationship disappeared when
 2794 including first harshness breadth in the model: occurrence in former Laurasia was not
 2795 significant (P varying 0.239 from to 0.294) while harshness breadth was significantly related

2796 to low clade rank (P varying from 0.001 to 0.002). Overall, this indicated that species using
2797 harsh environments are particularly bound to former Laurasia continents (above paragraph)
2798 and that - as a statistical consequence - we find many species of low clade rank on former
2799 Laurasia continents.

Reconstructions of ancestral states

The below graphs show the reconstructions of the three traits analysed for each of the six trees. Visiul inspection shows that the different trees lead to the same conclusions on which trait states are ancestral and when they have changed throughout evolution.

