

Phylogeny and classification of the genus-group taxa of *Loxandrina* (Coleoptera, Carabidae, Abacetini)

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Abstract

Bayesian and parsimony phylogenetic analyses of combined and partitioned datasets of molecular (partial sequences of 28S, wg, COI, and CAD) and morphological (51 characters of adults) data for exemplar taxa of five outgroup and 76 ingroup abacetine carabids resulted in a monophyletic *Loxandrina* Erwin & Sims, 1984 that is split into Australian and American clades. The genus *Loxandrus* LeConte, 1853 as previously delimited is not monophyletic relative to numerous genus-level taxa in Abacetini Chaudoir, 1873 and is restricted to a subgenus of North American species. A reclassification and nomenclatural changes for the subtribe that are consistent with the phylogeny are provided. Three genera are removed from *Loxandrina*: *Aulacopodus* Britton, 1940 moved to Pterostichini Bonelli, 1810; *Cosmodiscus* Sloane, 1907 and *Tiferonia* Darlington, 1962 moved to Abacetina. Based on the phylogenetic relationships and nomenclatural priority only four genera are recognized in *Loxandrina*: *Cerabilia* Laporte, 1867, *Zeodera* Laporte, 1867, *Pedimorphus* Chaudoir, 1878, and *Oxycrepis* Reiche, 1843. All other previously recognized genera are treated as subgenera. The classification change created eight secondary homonyms that are resolved by the proposal of the following: *Oxycrepis gebi*, replacement name for *O. balli* (Straneo, 1993); *O. amatona*, replacement name for *O. matoana* (Straneo, 1993); *O. xiproma*, replacement name for *O. proxima* (Straneo, 1993); *O. rasutulis*, replacement name for *O. suturalis* (Straneo, 1993); *O. laevinota*, replacement name for *O. laevicollis* (Bates, 1871); *O. arvulap*, replacement name for *O. parvula* (Straneo, 1951); *O. noaffine*, replacement name for *O. affinis* (Straneo, 1991); *O. alutona*, replacement name for *O. notula* (Tschitschérine, 1901). An overview of the morphological characteristics and diagnostic features of *Loxandrina* taxa is provided. A key and habitus images are provided for identification of genera and subgenera. The possible historical biogeography of the group is discussed in light of their phylogenetic relationships and past geological events.

Key Words

Australia, elytral striae homology, Gondwanan distribution, Ground beetles, South America

Introduction

For more than 100 years, coleopterists such as Bates (1872), Casey (1918), and van Emden (1949), have recognized the similarity among taxa related to *Loxandrus* LeConte, 1853, though no formal grouping was implemented in classifications by these early authors. Most publications simply maintained these constituent genera within a large, shifting concept of Pterostichini. It was not until Moore (1965) recognized an informal group of Australian and New Zealand genera as the *Loxandrus* series

within his concept of Pterostichinae that a more formalized approach to the definition a higher taxon began. Allen and Ball (1980) enumerated the generic composition of the *Loxandrus* series, expanding Moore's concept to include North and South American taxa. Allen and Ball discussed the basic features of adults presumed to be members, and made a case that it was possible that the *Loxandrus* series may represent a “fundamentally distinct group” from Pterostichini. Subsequently, Allen (1982) changed the composition of the included genera but did not provide character evidence for those changes. The

subtribe Loxandrina was established nomenclaturally by Erwin and Sims (1984) and then defined more explicitly as a tribe by Bousquet and Laroche (1993). Though there was a small, but growing body of evidence for recognition of a distinct group centered on *Loxandrus* and the affinity of these loxandrines to abacetines, some authors were appropriately cautious regarding the interpretation of the data available to them given the diversity of the taxa in this complex of genera. Straneo (1991) questioned the interpretation of character states and paucity of character data used to separate loxandrine taxa from pterostichines. He maintained that the distribution of the most obvious characters, such as the obliquely expanded male protarsi (Fig. 3A), absence of the “scutellar striole” (Fig. 2, see discussion of this term below) and defensive chemical compounds were too variable, of only “specific” value (i.e., useful at the species level) and/or subject to convergence due to ecological pressure. He preferred inclusion of loxandrines in larger concept of Pterostichini, however, no specific classification was presented. A preliminary, exemplar cladistics analysis of morphological characters (Will 2000) placed loxandrines and abacetines outside of Pterostichini s. str. counter to Straneo’s (1991) stance that the evidence was equivocal. However, that study did not provide strong evidence for the tribe’s monophyly, as character support was minimal and the set of taxa studied was very limited.

The possible association of loxandrines with abacetines (e.g., *Loxandrus* series of Allen and Ball (1980) + *Abacetus* series of Moore (1965), the Abacetini of Jeannel (1942a; 1948), and Abacetides of Chaudoir (1873)) has been suggested in a number of papers (van Emden 1949; Bousquet 1985; Arndt 1988; Straneo 1991; Bousquet and Laroche 1993; Bousquet 1999) and found in a cladistic analysis of morphological characters (Will 2000). Bousquet (2012) adopted the use of Abacetini as tribal name for the inclusive taxa, though he stated that Abacetini in his sense is “inadequately characterized” and that the “[m]onophyly of this tribe has not yet been demonstrated.” Nevertheless, he extended the Abacétides of Chaudoir (1873) to include Celioschesini of Jeannel (1948) and all Loxandrini sensu Erwin and Sims in his concept of Abacetini.

A rigorous analysis testing the monophyly and relationships at various levels for the abacetine-loxandrine complex has not been previously undertaken. In all preceding studies Loxandrina or Abacetini were only represented incidentally by a small sample of exemplars. Earlier works were necessarily restricted to a select fauna or loxandrines were not the central focus in those studies. Maddison et al. (1999) published studies using DNA sequence data that include a single exemplar of *Loxandrus*, that was consistently placed in Harpalinae, in a clade with *Agonum* Bonelli, 1810 and *Morion* Latreille, 1810. Also, Ober (2002, 2003) included exemplars of *Loxandrus* and *Abacetus* Dejean, 1828, that emerged as sister taxa in some analyses. The most extensive analysis based on DNA sequence data included exemplars of four Abacetini

genera that were found to be monophyletic, though with modest support (Ober and Maddison 2008).

Abacetini sensu Bousquet has over 800 described species (Lorenz 2005) distributed on all continental land masses except Antarctica (Fig. 21). Species diversity is highest in South America, which has exclusively Loxandrina taxa, and Sub-Saharan Africa with exclusively non-Loxandrina abacetines, herein referred to as Abacetina. Loxandrina is well represented in the Australian region and Abacetina is diverse across tropical Asia. These two groups are distributed exclusively except in the northern Australian bioregion and the very southern Oriental region, which is the only area where both subtribes co-occur. The species diversity greatly and rapidly diminishes north of South America, north of the Sahara in Africa, in southern Europe, and in northern Southeast Asia. This “south to north subtraction pattern” (Allen and Ball 1980) is consistent with the apparent Gondwanan distribution and a presumed Southern Hemisphere origin of the clade.

This contribution focuses on Loxandrina, which is found in the Australian region (Australia, New Caledonia, New Guinea, New Zealand, and Sulawesi) and in the New World (Argentina to southern Canada) using exemplar Abacetina taxa to test the monophyly of the subtribe Loxandrina. The purpose of this study was to determine what genera should be included in the subtribe, to test their monophyly in a phylogenetic framework using a combined, multi-locus DNA and morphology dataset and to devise a new, evidence-based classification that is compatible with well-supported phylogenetic relationships.

Methods

Monophyly of Abacetini and exemplar taxa selection for phylogenetic analysis

As a starting point, it is necessary to establish a reasonable working hypothesis of Abacetini monophyly exclusive of other Harpalinae tribes. To do this, a parsimony analysis was done using an unpublished dataset with over 500 taxa from across Carabidae, the vast majority being in Harpalinae, Pterostichini, and Abacetini. This large preliminary screening used an exemplar dataset including partial sequence data for three loci: 28S, wg and CAD, and a partially coded matrix of about 100 morphological characters (Will unpubl. Data). Exemplars of all the major abacetine genera that were included in this analysis form a clade separate from Pterostichini (including *Aulacopodus* Britton, 1940 discussed below) and other Harpalinae tribes. The clade is always rooted between *Abacetus* and the other abacetine taxa. Study of the morphology of dried specimens and descriptions from the literature indicate that the remaining Abacetina (non-Loxandrina taxa as listed by Lorenz (2005)) are unlikely to be closely related to any Loxandrina taxon included here, but may form a paraphyletic grade leading to Loxandrina. Based on this, exemplars from *Abacetus*, *Inkosa* Péringuey, 1926,

Cyrtomocelis Chaudoir, 1874 and *Metabacetus* Bates, 1892 were included as outgroup taxa in the present analysis.

The two included species of *Abacetus* represent crown-group Abacetina, i.e., species with the following combination of features: antennomere 2 inserted eccentrically to antennomere 1, very short, transverse mentum, stridulatory structures on the proepisternum, and deeply impressed clypeo-ocular sulci. Each of the other Abacetina taxa, *Inkosa*, *Cyrtomocelis* and *Metabacetus*, lacks one or more of those features and are placed in the broader concept of Abacetini as incertae sedis, but are, for convenience and as a working hypothesis referred to as being in Abacetina. Currently there is no evidence that Abacetina taxa form a clade beyond *Abacetus* and its close relatives. All of the morphological features listed above for these Abacetina genera, except for a somewhat transverse mentum, are absent from all *Loxandrina* taxa.

The putative in-group terminals included in the analysis are exemplars from all recognized loxandrine genera from the New World and Australian region. Many genera are monotypic or have very few species, but *Loxandrus* auct. has more than 200 species and *Cerabilia*, more than 50. From these larger genera the exemplars included cover the apparent morphological diversity, most of the informal groups previously recognized (Allen and Ball 1980; Straneo 1991; Bousquet 2006) and the geographic range of the genus-level groups. Likewise, the *Cerabilia* species included here are a subset of the more than 60 species in the genus, most from Australia and New Caledonia.

Both DNA (minimum of two loci of the four sought) and morphological data are included for all taxa with the only exception being *Zeodera (Haploferonia) simplex* (Darlington, 1962), which is only known from the holotype specimen. For that species only morphological data is available. The full matrix includes 81 OTUs (operation taxonomic units (Sokal and Sneath 1963)).

Specimens examined

The basis of this study has been built over the last more than 20 years by studying and taking numerous specimens of Abacetini on loan for examination, including types, from the holdings of the following collections:

- AMS** Australian Museum, Sydney;
- ANIC** Australian National Insect Collection, Canberra;
- CASC** California Academy of Science, San Francisco, CA;
- CMNH** Carnegie Museum of Natural History, Pittsburg, PA;
- CUIC** Cornell University Insect Collection, Cornell University, Ithaca, NY;
- EMEC** Essig Museum of Entomology, Berkeley, CA;
- MCSN** Museo Civico di Storia Naturale “Giacomo Doria”, Genova;
- MCZ** Museum of Comparative Zoology, Cambridge, MA;

- MNHN** Muséum National d’Histoire Naturelle, Paris;
- NHM** The Natural History Museum, London;
- NZAC** New Zealand Arthropod Collection, Auckland;
- QDAF** Queensland Department of Agriculture and Fisheries, Brisbane;
- QM** Queensland Museum, Brisbane;
- SAMA** South Australian Museum, Adelaide;
- USNM** National Museum of Natural History, Washington, DC;
- WAM** Western Australian Museum, Perth;
- ZMS** Zoologische Staatssammlung, München.

Many of the specimens examined are enumerated in various publications on Abacetini (e.g., Will and Liebherr 1997; Will 2004, 2005, 2008, 2011, 2020a, 2020b; Will and Park 2008).

Based on these museum specimens, of the 343 currently named species-level taxa in *Loxandrina* I have studied in detail or at least made a cursory examination of identified exemplars of 247. Described species represented in material I have examined are indicated in the supplementary file (Suppl. material 1). Not all taxa have been studied to the same level of detail and this is roughly indicated in supplementary file 1 with the following codes: H= holotype, lectotype or syntypes seen and in most cases additional material beyond the type(s) was also studied; P= paratype(s) seen and additional material for most taxa. The exclamation point “!” indicates that I studied confidently identified material determined by people that have published revisions of loxandrine taxa, e.g., Sloane, Ball, Allen, or Straneo, or this is material that I have identified using published keys and descriptions, but without recourse to the types. For specimens in the MNHN, largely the Bates and Tschitschérine collections, I have marked species with the exclamation point. However, it is almost certain that the specimens I examined are the types. I have not indicated them as such because when I examined those specimens I only took a low-resolution dorsal image and made notes regarding character states and I did not make a careful record of the labels and localities, information essential to establishing these are in fact the types, nor have I designated them as lectotypes. The entries with asterisks are taxa included in the phylogenetic analysis. These have been studied through careful examination, dissection and DNA extraction as much as possible. Based on the breadth of material I have examined and the DNA data screening used for taxon selection as described above, I believe that the exemplars are a good sample of the major lineages currently described.

Of the remaining species that I know only from descriptions, nearly all are adequately described such that there is no doubt of their inclusion in *Loxandrina* and it seems extremely unlikely that any of those represent a lineage worthy of genus-level recognition. Based on museum material I have studied there are many undescribed species in the subtribe. *Oxycrepis* alone appears to have many dozens of undescribed species from the New World.

Morphological character analysis methods

Observations of anatomical features were made using a Leica MZ12s stereomicroscope or similar. Measurements were made using an ocular reticle. Habitus photos of beetles were taken as image stacks using a modified Microptics XLT digital imaging system that were then aligned and assembled with Helicon Focus version 5.3 and those image files were edited to enhance clarity using standard image editing software.

A total of 51 morphological character are used in the phylogenetic analysis. The characters and character states are discussed and detailed in the morphology section below, divided by body tagma, and with continuous numbers as they appear in the matrix. Most characters (32) are binary. Multistate characters were treated as unordered in the parsimony analysis. The morphology matrix is largely complete, with only three characters of the female tract not scored for 19 OTUs in which the female is unknown or has not been studied and similarly, four OTUs are not scored for male leg and aedeagus characters. The full matrix is included as a Mesquite file on Data Dryad (<https://doi.org/10.6078/D10411>).

Male genitalia and female tract preparations. Specimens were relaxed either by placing them in near-boiling distilled water with a drop of dishwashing detergent for about 30 min or by placing them in a relaxing chamber with water and chlorocresol for one to three days. For the female reproductive tract the entire abdomen was removed and invaginated tergites and sternites connected to the female reproductive tract removed. Male genitalia, typically including the ring sclerite, was extracted from abdomen. For both males and females soft tissues digested by placing the sample into room temperature, 10% KOH or by placing the sample in a pancreatin solution (Alvarez-Padilla and Hormiga 2008), held in a warming oven at 37 °C overnight or up to 24 hrs. For KOH digestions the dissected samples were washed in 4% acetic acid for 5 min. All samples were washed with distilled water. Female reproductive tracts were stained in a solution of chlorazol black and processed using the same methods as used by Liebherr and Will (1998). After washing and staining samples were placed in glycerine-filled genitalia capsules.

DNA sequencing

Abbreviations used for loci and their aligned length in the matrices are as follows: 28S: 28S ribosomal DNA (1297bp); COI: cytochrome oxidase I, (851bp, JER-PAT primer region (COI_{jp}), 707bp, HCO-LCO region (COI_f)); wg: wingless (529bp); CAD2: carbamoyl phosphate synthetase domain of the rudimentary gene (931bp). Fragments for these genes were amplified using polymerase chain reaction, exo-sap cleaned and sequenced following the same procedures and primers given by Will (2015a). Assembly of multiple chromatograms for each gene fragment and initial base calls were made with Phred (Green and Ewing 2002)

and Phrap (Green 1999) initiated within Mesquite's (Maddison and Maddison 2018b) Chromaseq package (Maddison and Maddison 2019) with subsequent editing done by manual inspection within Mesquite. Multiple peaks at a single position were coded using IUPAC ambiguity codes. Sequences have been deposited in GenBank with accession numbers: 28S MT849608–MT849681; CAD2 MT849530–MT849607; COI_f MT849682–MT849760; COI_{jp} MT849451–MT849529; and wg MT849381–MT849450 (Suppl. material 2). Primary collection data for voucher specimens of all sequenced are deposited in the EMEC public database at <https://essigdb.berkeley.edu/>.

The matrix is complete for all loci for 72 of the 80 terminals where material was available for DNA extraction. At least two loci were required for inclusion in the dataset. The few lacking loci are: wg- *Cerabilia edentata* Will, 2020, *C. montivaga* Will, 2020, and *Zeodera lata* (Darlington, 1962); 28S- *C. iridescens* Will, 2020 *C. spinifer* Will, 2020 and *Z. subiridescens* (Macleay, 1871); COI- *C. orbiculata* Will, 2020 and *Oxycrepis epiphyta* (Will, 2004); CAD2- *C. spinifer* and *O. epiphyta*. All sequences are of approximately the lengths given above with a few exceptions. The 28S sequence for *Pediomorphus obtusus* Will, 2019 failed to sequence clearly for the d3i primer and the included sequence ends at aligned position 804 and is derived from the d1 primer. Similarly, *C. klin-gonorum* Will, 2020 failed to sequence for CAD2 for the CD668R primer and the 462bp included are derived from the CD439F primer only.

DNA sequence alignment

Alignment of the protein-coding sequences was straightforward with the only insertions or deletions in wg in the region of the aligned position 170–193 representing two to four amino acids. Multiple sequence alignment of 28S was performed by MAFFT (Kato and Standley 2013) using default parameter values within Mesquite. Gblocks vers. 0.91b (Castresana 2000; Talavera and Castresana 2007), selection algorithm was used to select regions of the aligned 28S data that have highly ambiguously alignments. The selected 285 characters of 28S were excluded from the analysis. Parameters used for Gblocks are included with all input and output files for all analyses on Data Dryad (<https://doi.org/10.6078/D10411>).

Phylogenetic analyses

All matrices, input files, script files, and output files for all analyses are included on Data Dryad (<https://doi.org/10.6078/D10411>).

Three Bayesian analyses were done; 1. the 80 OTU matrix with sequence data and morphological data, 2. the 80 OTU matrix with sequence data alone, and 3. the 81 OTU matrix that also includes *Z. simplex*, represented in the matrix only by the morphology of

the holotype. Models of nucleotide evolution were chosen with the aid of mrModelTest (Nylander 2004) and PAUP* (Swofford 2002). Using the hierarchical likelihood ratio test and Akaike information criterion (Akaike 1973) the chosen model was GTR+I+ Γ for the COI_f, wg, and 28S partitions and HKY+I+ Γ for COI_{jp} and CAD2. The morphology partition was run under symmetric model in which the frequency of each state is equal and all characters informative. Analyses were done with a matrix of the four-gene and morphological partitions concatenated together. Bayesian analyses were conducted using MrBayes ver. 3.2.7, (Ronquist et al. 2012) parallel version (Altekar et al. 2004). To ensure an average standard deviation of split frequencies (ASDSF) below 0.01 was achieved (Ronquist et al. 2009), and that likelihood scores and all parameter values reached a stable plateau, an initial analysis was run using the command “stoprule = yes” with “stopval = 0.009998.” Tracer (Rambaut et al. 2018) was used to examine trace files resulting from this run and the effective sample size (ESS) of the parameters used to assess convergence and stationarity. For each analysis, the trees in a burn-in period of 25% of the generations were excluded. While the ASDSF went below 0.01 in only 1.5 million generation for the initial analysis, the ESS values for a few parameters were still below 200, the rule of thumb threshold (Nascimento et al. 2017). The stop value command was removed and a second analysis of 5 million generations for four runs of eight chains was conducted. This analysis reached an ASDSF of 0.0047 (analysis 1, 80 OTUs), 0.0060 (analysis 2, 80 OTUs), and 0.0099 (analysis 3, 81 OTUs) and all ESS values >1000 in all analyses. The majority-rule consensus tree of post-burn-in trees was calculated to determine Bayesian posterior probabilities (PP) of clades.

A parsimony analysis of the morphology partition for all 81 OTUs was done. The matrix was submitted to TNT parallel version (Goloboff et al. 2008; Goloboff and Catalano 2016) using the Zephyr ver. 2.11 package (Maddison and Maddison 2018a) in Mesquite. Five replicates using TNT’s fusion, drift, ratchet methods, with maxtrees 10,000, was done on each of the 32 processors. Full TNT commands used for the heuristic searches are included in files on Data Dryad (<https://doi.org/10.6078/D10411>). The parsimony analysis examined 59.9 trillion rearrangements and filled the maximum of 10,000 trees on all runs.

Results

Phylogenetic results

The resulting trees from the Bayesian analysis of the combined data (analyses 1 & 3, (Suppl. material 3)) are identical except for very slightly lower posterior probability (PP) values for some clades in analysis 3, which included *Z. simplex* (Fig. 1). Analysis 2, the sequence data only matrix, also largely has the same topology but differs no-

tably in not recovering a monophyletic *Cerabilia*. Clades corresponding to recognized genera and subgenera that are supported by the sequence data only analysis (analysis 2) are indicated with a diamond in figure 1.

The parsimony analysis of the morphological matrix for all OTUs resulted in shortest trees of 227 steps and a strict consensus tree that was largely unresolved (Suppl. material 3). The lack of resolution is expected given the small number of characters; however, *Pedimorphus*, *Cerabilia* s.l., *Cerabilia (Biliacera)* and clades within *Biliacera* were all found to be monophyletic in the strict consensus of the set of most parsimonious trees. The parsimony analysis placed *Z. (Haploferonia) simplex* in a clade of *Zeodera* species together with *Z. (Nebrioferonia) strigitarsis* (Straneo, 1939) and *Z. (s. str.) atra* Laporte, 1867. Clades supported by the morphology data only analysis are indicated with a star in figure 1.

Given that the analyses are generally compatible, the resulting tree from the combined matrix including all OTUs (Fig. 1) is considered the preferred hypothesis for the relationships for the genera and subgenera and is the basis for all further discussion and taxonomic and nomenclatural changes. This phylogeny includes a well-supported *Loxandrina* with two clades, the New World *Oxycrepis* clade and the Australian region clade of *Cerabilia*, *Pedimorphus*, and *Zeodera*. *Oxycrepis* is then further divided into a clade of *Oxycrepis (Loxandrus)* species, which includes only North American and Antillean species and is sister to the clade of the remaining *Oxycrepis* species. The latter clade is exclusively Central and South American species and includes all the remaining New World subgenera that were previously treated as genera within the subtribe. Each of these subgenera is relatively highly derived within the tree and are mixed among many species that are considered typical looking “*Loxandrus*” species. Both species of *Adrimus* Bates, 1872 included are found to be sister species. All four *Stolonis* Motschulsky, 1866 species that were included form a derived clade together with a peculiar and presently undescribed species best categorized as a member of Straneo’s group-17 (Straneo 1991). The *Stolonis* clade and the single species of *Oxycrepis* s. str. are included in a polytomy with a clade of other, rather large-sized, South American species and the single included *Metoncidus* Bates, 1871 species.

The clade of taxa from the Australian region includes *Cerabilia* as sister to *Zeodera* + *Pedimorphus*, which are each reciprocally monophyletic. *Zeodera* includes all taxa formerly included in *Loxandrus* from the region and all the *Zeodera*-like New Guinea genera, *Nebrioferonia* Straneo, 1939, *Haploferonia* Darlington, 1962, and *Homalonesiota* Maindron, 1908. *Cerabilia* includes an exclusively New Caledonian clade, subgenus *Biliacera* Will, 2020, which contains a derived clade of *Cerabilia (Biliacera) inversa* Will, 2020, *C. (B.) klingonorum*, *C. (B.) letalis* Will, 2020, *C. (B.) sternovillosa* Will, 2020, *C. (B.) vitalis* Will,

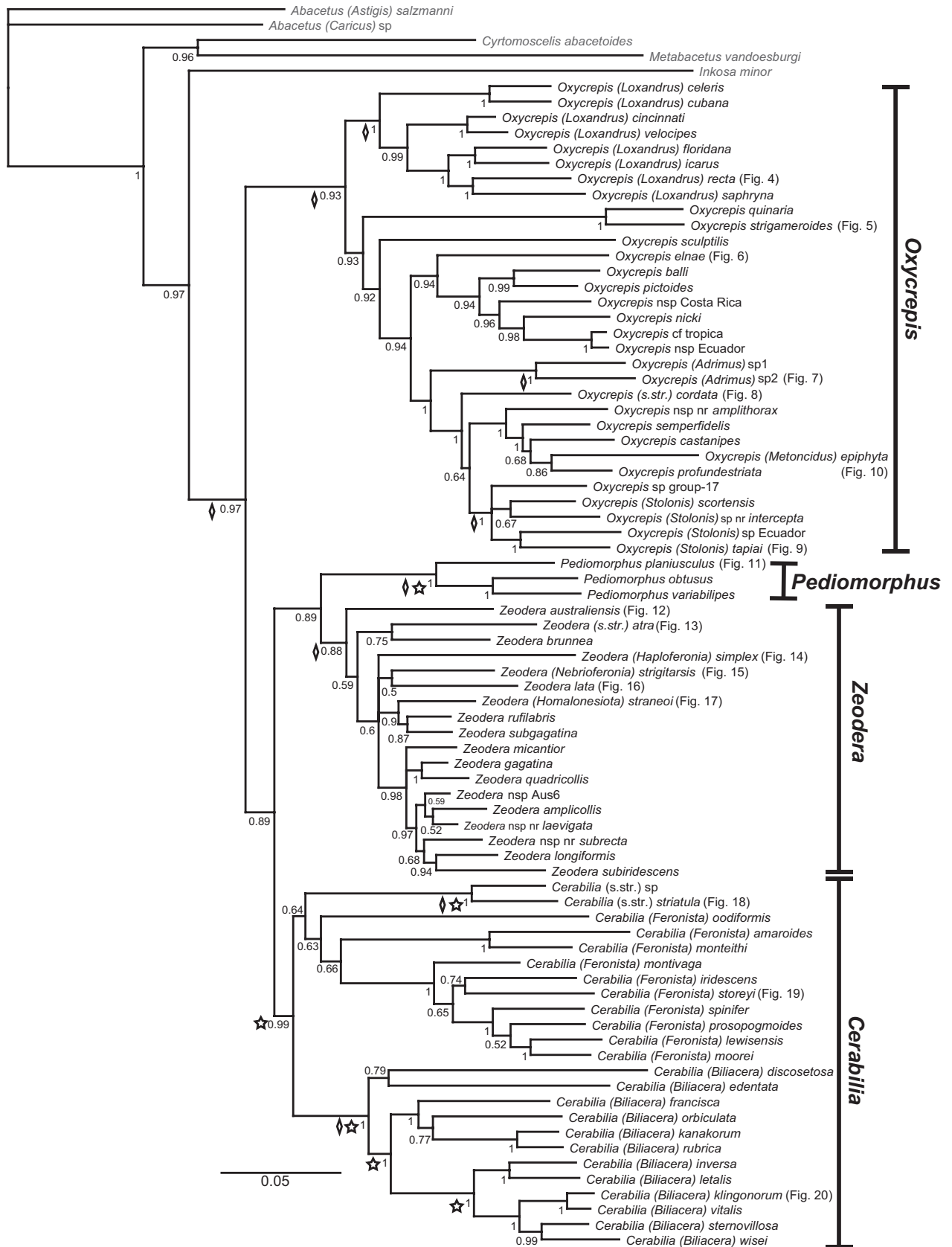


Figure 1. Phylogeny of Loxandrina inferred from a Bayesian analysis of the combined dataset (analysis 3). Numbers at nodes are posterior probability values (PP). Stars at nodes mark clades found in a parsimony optimality analysis using the morphology partition. Diamonds at nodes mark recognized genera and subgenera inferred from a Bayesian analysis of the sequence data partition (analysis 2).

2020, and *C. (B.) wisei* Will, 2020, which all share an inverted – right side up – position of the aedeagus when in repose. All Australian *Cerabilia* are in the subgenus *Feronista* Moore, 1965 and are placed in a single clade, though with rather modest support (PP 0.63).

Results of morphological character analysis and recognition of *Loxandrina* taxa

Many species of the tribe have a generalized form that is similar to species of Platynini or Harpalini. They are generally, but not universally, separable from these taxa by lack of the angular base of stria 1 (Fig. 2D) and presence (in most) of the plica at the elytral apex. Additionally harpaline species have only a single supraorbital seta, while two are always present in loxandrines.

Most tribal-level keys will trace loxandrines to Pterostichini (e.g., Erwin 1991; Lawrence and Slipinski 2013), with the exception of some recently published keys (Baehr and Will 2019; Ball and Bousquet 2000). For the purpose of identification, separation of loxandrine taxa from pterostichine taxa is based on a combination of characters: Harpalinae that lack the angular base of stria 1; elytral apex is entire not truncate; antennae are filiform; mouth parts with few setae; suture medially between mentum and submentum distinct; abdominal ventrites without any deep punctures in a transverse row nor any impressed transverse sulci; tarsal claws smooth; dorsally, never with prominent metallic color; two supraorbital setae (among Abacetini single supraorbital setae only known in *Tiferonia brunnea* (Jedlička, 1935) and *Abacaecus walterossi* Allegro & Giachino, 2020). All these characteristics are either likely plesiomorphies or absence character states (see also key to genera below). The character state combination and gestalt allow for recognition of loxandrine member taxa, but provide no unreversed synapomorphies for the group.

Characters discussed below have been used by at least some previous authors and most were presented by Allen and Ball (1980). I discuss their variation, utility for identification, and then introduce the characters scored for the phylogenetic analysis within the appropriate tagma.

General habitus: Figures 4–20. *Loxandrina* species include beetles of middling size, 3–22 mm long, (typically about 8 mm). Most are glossy and have a distinct spectral iridescent on some or nearly all of the body. They are typically piceous to deep brown, or deep black throughout the body, frequently with contrastingly paler legs and mouth parts. Many *Oxycrepis* have various patterns of red or flavous spots or vittae on their elytra (Fig. 6), some with contrastingly pale legs, and white and black antennal segments (Figs 8, 9). Species from the Australian region have no distinct pale markings or, rarely, at most, they have a paler apical region on the elytra, a paler elytral interval 1, or very obscurely paler humeri. In general form, most species are rather typical looking Harpalinae, often resembling an average Platynini, Harpalini or Pterostichi-

ni species. Exceptional body forms have usually been recognized as genera or subgenera and are discussed below.

The majority of species, primarily members of *Oxycrepis* and *Zeodera*, have the microsculpture of the dorsum, on one or more body region, with microlines that cause an iridescent reflection, i.e. diffraction gratings (Seago et al. 2009). Use of variation in apparent microsculpture was best investigated by Allen and Ball (1980) for Mexican *Oxycrepis*. That study suggested that characteristic microsculpture may be useful at the species/species-group level, and should be further explored in the context of a complete species-level revisions. In addition to potential phylogenetic information it is possible that there is a correlation between microsculpture form and habitat (Allen and Ball 1980). There is no obvious grouping information in this system at supra-generic level, however. The directional transformation as suggest by Allen and Ball of reticulate to transverse remains equivocal given uncertainty as to the ancestral condition for the subtribe.

Head: The structure and form of the head varies little across all loxandrine taxa. The head is moderately elongate, mandibles moderately prominent and slightly curved. Palpi are fusiform and have very few setae, except in *Pedimorphus*, where the apical labial palpomeres are enlarged, setose and bear a ventral sensorium (Will 2019), and in some *Cerabilia* (*Biliacera*) species that have plurisetose palps (Will 2020b). Eyes are always present and usually prominent, but are rarely quite small and flat as in some *Cerabilia*, moderate sized as in most *Oxycrepis* or exceptionally large as in some *Oxycrepis*, notably in *O. oophagus* (Costa & Vanin, 2011), *O. quinarius* (Will & Liebherr, 1997), *O. strigomeroides* (Straneo, 1991) (Fig. 5) and some species in the subgenus *Adrimus*. The dorsum of the head has two pairs of supraorbital setae. Antennae are filiform, elongate, and usually fully pubescent from antennomere 4 except in some species of *Cerabilia* that have pubescence starting on antennomere 3.

In Abacetina a very short, transverse mentum is common. Some *Loxandrina* approach this condition but are never as short as in many *Abacetus* species where the epilobes are less prominent than the medial tooth (Moore 1965, his fig. 10). *Loxandrina* includes the full range of mentum form, from very short and transverse to relatively elongate with the epilobes as or more prominent than the medial tooth. The mentum tooth is usually entire and more or less pointed at the apex. However, blunt, truncate or very slightly emarginate forms are known. The paramedial pits of the mentum also vary from absent to large and deeply impressed. Rarely the pits are large and setose as in some species of the subgenus *Biliacera*. Variation of the mental pits is known within certain species (Allen and Ball 1980: 550). The mentum appears to provide useful variation for identification at the species level; however, it does not group taxa at higher levels.

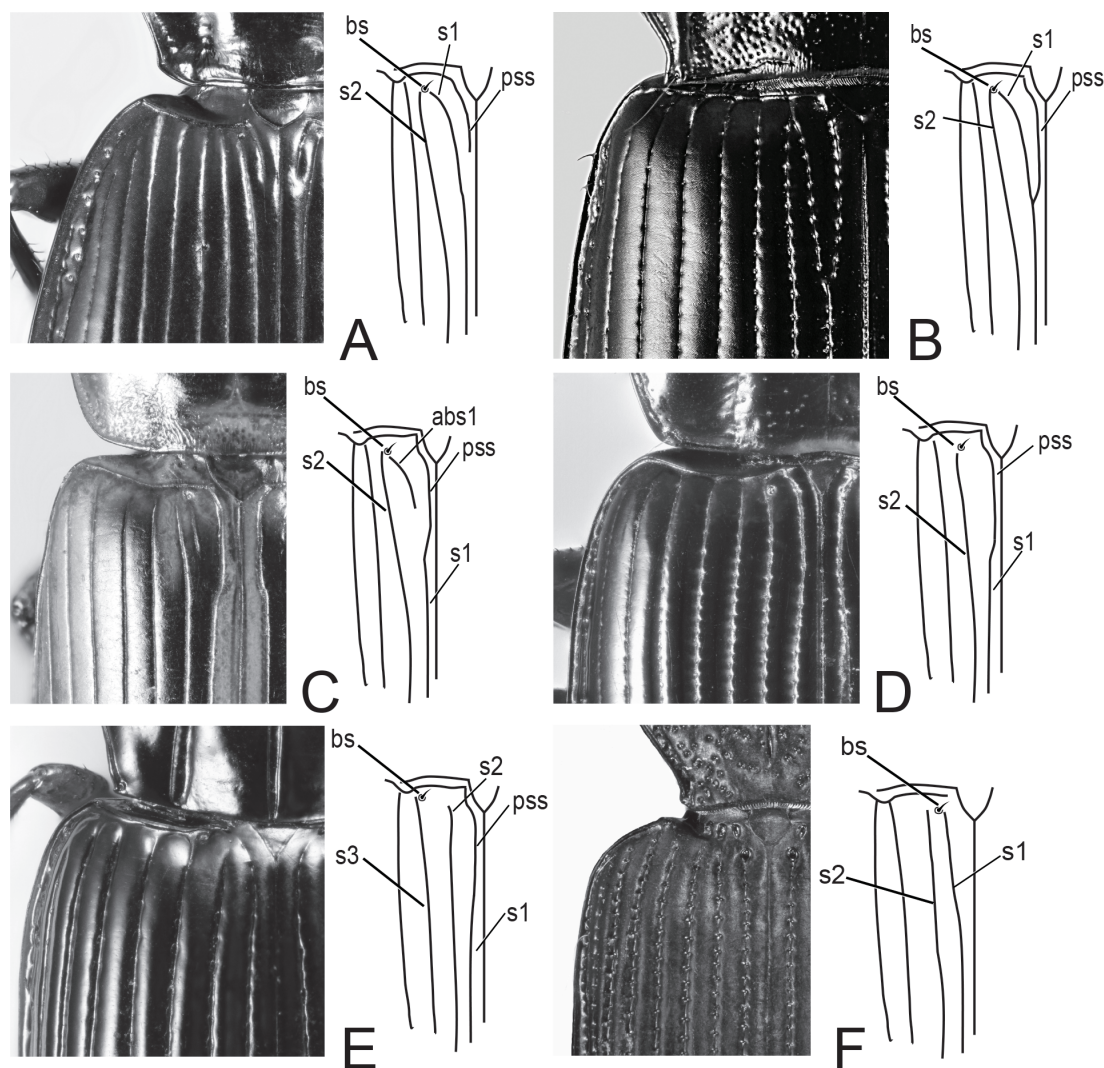


Figure 2. Basal portion of the left elytron paired with a labeled, schematic representation of configurations of striae and basal setae. Schema after Baehr and Will 2019. s1- stria 1. s2- stria 2. s3- stria 3. pss- parascutellar stria. bs- basal setigerous puncture. abs1- angular base of stria 1. Each image represents a unique state: **A.** Stria 1 entire and parascutellar striole free. *Platynus ovipennis* (Motschultsky 1845) (Platynini); **B.** Stria 1 entire and parascutellar striole joined to stria 1. *Amara (Curtinotus) carinata* (LeConte 1847) (Zabrini); **C.** Angular base of stria 1 free and parascutellar striole joined to apical portion of stria 1. *Stenolophus (Agonoderus) maculatus* (LeConte 1869) (Harpalini); **D.** Angular base of stria 1 absent and parascutellar striole joined to apical portion of stria 1. Basal setigerous puncture near stria 2. *Oxycrepis (Loxandrus) recta* (Say); **E.** Angular base of stria 1 absent and parascutellar striole joined to apical portion of stria 1. Basal setigerous puncture near stria 3. *Caelostomus* sp. from Indonesia (Drimostomatini); **F.** Parascutellar stria absent, stria 1 entire. *Melaenus piger* (Fabricius 1801) (Melaenini).

Head characters and character states used in the phylogenetic analysis

1. Antennae basal segments- [0] antennomeres 1 and 2 glabrous, 3 pubescent in at least the apical third, usually more; [1] antennomeres 1 to 3 glabrous except for a few long setae near the apices. Typically abacetine taxa have antennomeres 1 and 2 glabrous as in state 0. Among species included here, only a few *Cerabilia* have the entire antennomere 3 glabrous.
2. Antennomere 2- [0] symmetrically inserted into antennomere 1; [1] asymmetrically inserted into antennomere 1. Among species included here, only *Abacetinus* species have the distinctly asymmetrically inserted

antennomere 2. This is typical of that genus and many taxa considered to be members of Abacetina. This was considered a key characteristic of Abacetini sensu Jeannel (1948) exclusive of his *Celioschesini*.

3. Clypeal-ocular sulcus- [0] punctiform and moderately deep or slightly elongate, but then very short and shallow; [1] clearly linear, broad, shallow and not well defined; [2] well impressed, linear, reaching or nearly reaching anterior supraorbital seta. Almost all *Loxandrina* have punctiform impressions on the head as in state 0. Many, probably most Abacetina have state 2 and this is widely, though not perfectly correlated with having antennomere 2 asymmetrically inserted into antennomere 1 (Character 2, state 1).

4. Apical labial palpomere form- [0] fusiform to acuminate, lacking ventral sensorium; [1] enlarged, subglobose with ventral sensorium (Will 2019). The subglobose palpomere with a ventral sensorium is only found in *Pediomorphus* species.
5. Mentum tooth shape- [0] entire, triangular tooth; [1] emarginate at apex; [2] truncate at apex; [3] tooth absent. The majority of Abacetini species have a simple tooth (state 0). The absence of the tooth is an autapomorphy for *Cerabilia* (*Biliacera*) *edentata*. Those taxa with states 1 and 2 are few and the emargination is never so deeply pronounced as to be bifid such as is the state in some *Pterostichus* Bonelli, 1810 or *Notonomus* Chaudoir, 1865 species.
6. Microsculpture of dorsal surface of head- [0] not apparent at 50× magnification; [1] visible as isodiametric, irregular mesh of sculpticells; [2] visible as transversely elongate sculpticells.
7. Supraocular region- [0] smooth; [1] with two to many deep rugosities. Prominent rugose areas above and behind the eyes are only found in some species of *Cerabilia* (Will 2020b).

Thorax and legs: The form of prothorax is quite variable, but is typically slightly transverse or quadrate with the margins arcuate for their most of their length and somewhat sinuate in the basal half. Rarely the base of the pronotum is greatly constricted and the sides prominently rounded as in the subgenera *Oxycrepis* s. str. and *Stolonis*. Elytra are normally not fused and the flight wings are typically fully developed, i.e. large enough to have an apically folded region. However, flight wing reduction has occurred in many taxa e.g., all *Cerabilia*, some *Zeodera* (e.g., *Z. atra*, *Z. simplex*) and some North American *Oxycrepis* (Will and Liebherr 1997). Elytral striae are usually well impressed, the angular base of stria 1 (abs1) is uniformly absent (Fig. 2D), the parascutellar setigerous puncture is at the basal origin of stria 2 and a single dorsal puncture on the median disc of the elytron is in interval three (absent only in *Cerabilia* (*Feronista*) and *Pediomorphus* spp.). The unusual case of supernumerary setae on the elytra in odd-numbered intervals or a generally distributed short pubescence is found in some of the *Oxycrepis* subgenera as discussed below. Legs are moderately long, and relatively lightly built as compared to the stout legs of, for example, *Notonomus* or *Pterostichus*. Males frequently have the protarsi distinctly, asymmetrically expanded (Fig. 3A), with prominent squamose ventral setal pads. The asymmetry may be slight, or they may be narrow and symmetrical (Fig. 3B), as in some species of *Adrimus*. It is very common for males to have much larger, more ovoid profemora than females. The metatibiae have rows of fine to large setae. In *Cerabilia* these tibial setae are very large and stout, and the tibia is noticeably arcuate, especially in males.

The terms “scutellar striole,” “abbreviated stria,” “parascutellar striole,” and their variants in non-English languages, have been used to refer short striae near the

scutellum or in the region of stria 1 or 2. However, these terms do not necessarily refer to homologous structures across all groups and are not consistently used by various authors. Given that both the base of stria 1, whether connected to the rest of stria 1 (Fig. 2A, B, F) or not (Fig. 2C), and the parascutellar striole are simultaneously present in many taxa (Fig. 2A–C), so clearly not homologous, it is highly problematic that the same terms have been used in reference to both.

In beetle elytra the path of the tracheal trunks, main nerves, and flow of hemolymph is through wing veins. These veins are homologous across pterygotes and arranged, from the suture to the lateral margin: 2nd anal, 1st anal, cubitus, media, radius, subcosta+costa (Crowson 1981, his figs. 36, 37; Jeannel 1926, his fig. 95). Each vein is usually represented externally by an apparent interval of the elytron. Typically, these correspond to intervals 1 (=2nd anal), 3 (=1st anal), 5 (=media), 7 (=radius), and 9 (=subcosta+costa). A lattice of cross-veins between these main, longitudinal veins underlays the additional, 2–8 even numbered, apparent intervals that are between those representing the homologous veins.

The 2nd anal vein (interval 1) is branched basally, forming the parascutellar striole between its two branches. The parascutellar striole originates at the elytral base near the scutellum. In most carabids the parascutellar striole is relatively short. However, in some, such as most Migadopini, the parascutellar stria is nearly the length of the elytra, joining stria 1 in the apical third. In such cases the first two apparent elytral intervals actually correspond to the branches of the 2nd anal vein.

The stria that forms the boundary between interval 1 and interval 2 is referred to as stria 1. At the point that interval 1 (2nd anal) branches, stria 1 angles away from its path that is otherwise parallel to the suture as its origin is near the basal setigerous puncture, usually close to or joining stria 2. When this basal section of stria 1 is interrupted (Fig. 2A) it is present as a striole that is referred to as the angular base of stria 1 (abs1).

The parascutellar striole is directly adjacent to the scutellum on the elytra and continuous with the basal marginal border of the elytra when the border is evident (Fig. 2A–E). The basal section of stria 1, whether interrupted (Fig. 2C) or continuous with the apical portion of stria 1 (Fig. 2A, B, F) is the angular base of the stria.

In all abacetine taxa, elytral stria 1 is joined with the parascutellar striole and the angular base of stria 1 is absent (Figs 2D, 4–20). In most cases the width of interval 1 narrows slightly toward the base indicating the point at which stria 1 and the parascutellar striole join. Even in cases where the parascutellar striole and stria 1 are joined in a straight line (no noticeable change in interval 1 width) the basal origin of the parascutellar striole is distant from the basal elytral setigerous puncture and far from stria 2, indicating it is the parascutellar striole and not a complete stria 1 (compare Fig. 2D, F).

A single setigerous puncture on interval 3, often touching stria 2, is found in nearly all loxandrine taxa. An impunctate elytron is only seen in Australian *Pediomorphus* and the subgenus *Feronista*. Multiple

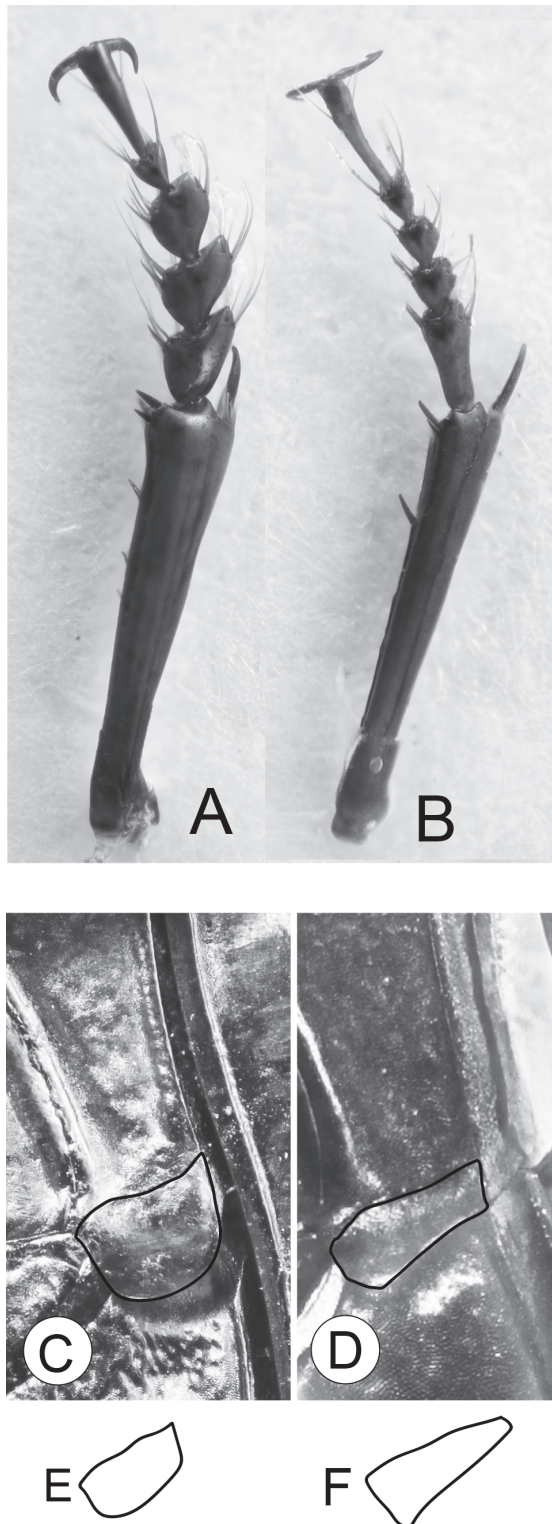


Figure 3. Protarsomeres and metepimera. Male left tibia and protarsomeres: **A.** *Oxycrepis (Loxandrus) recta* (Say). Asymmetrically expanded, as in typical many *Loxandrina* species; **B.** *Oxycrepis (Adrimus) gebi* Will narrow, symmetrically, slightly expanded. Metepimera, left side: **C.** *Oxycrepis (Loxandrus) recta*. Large, elongate, apically rounded form, as in typical *Loxandrina* species. Black outline added to emphasize shape; **D.** *Oxycrepis (Adrimus) rasutulis* Will. Rectangular, narrow, truncate form, black outline added to emphasize shape. Drawings of alternative metepimera shapes: **E.** short, apically rounded form; **F.** narrowly triangular, truncate form.

setae on interval three and other intervals as well, has arisen multiple times in the South American taxa, e.g., *Oxycrepis* s. str., *Metoncidus*, *Stolonis*, group-17 species of Straneo (1991), and the New Caledonian subgenus *Biliacera*. Overall in Carabidae the number of dorsal setae on the elytra is highly variable. However, considering the large number of species of loxandrines and abacetines it is remarkably stable for these taxa, particularly, if one compares the limited variation in loxandrines to the broad range of setal number in genera such as *Pterostichus*.

A single, linear basal impressions of the pronotum on each side is the typical state for both Abacetina and *Loxandrina* taxa. However, these impressions may also be punctiform, broad and shallow, or even absent or nearly so (e.g., many *Cerabilia* species). No loxandrine taxa have both a medial and lateral impression on each side such as is found in various pterostichine taxa such as, *Pterostichus* and *Prosopogmus* Chaudoir, 1865.

Obliquely dilated protarsomeres in males is a feature that is found in many loxandrine taxa with notable exceptions in species from several genera and subgenera including *Adrimus*, *Metoncidus*, *Cerabilia* and some *Oxycrepis*. The usual tarsomere form is asymmetrically expanded and somewhat cordate (Fig. 3A) with the apicomedial lobe roundly produced beyond the lateral lobe. This differs from the common form of male tarsomeres found in most carabid taxa; cordate or truncate and nearly symmetrically shaped. The notable asymmetry in loxandrines is unlike the asymmetrically produced spinous processes found in both sexes of various Harpalinae and Abacetina taxa, e.g., *Brachidius* Chaudoir, 1852 and *Cosmodiscus* Sloane, 1907. However, in many pterostichines the male protarsomeres are not perfectly symmetrical, or even clearly asymmetrical (e.g., *Notonomus (Loxodactylus) carinulatus* (Chaudoir, 1865)). Well-developed tarsal asymmetry is also found in *Chlaeminus* Motschulsky, 1865 which is otherwise a typical Abacetina. Obliquely dilated male protarsi probably is a primitive characteristic for the loxandrine clade, however, it is difficult to score the state for some taxa and the phylogeny suggests repeated return to symmetry (Fig. 3B), apparently reversals.

Thoracic and leg characters and character states used in the phylogenetic analysis

8. Elytra basal, parascutellar setigerous puncture- [0] absent; [1] present at base of stria 2 or between striae 1–2. The majority of Abacetini have the parascutellar puncture and, when present, it is always at the base of stria 2 or between 1 and 2, which differs from the state in Drimostomatini, where it is placed at the base of stria 3 or between 2 and 3 (Fig. 2E). Both states coded here are found among *Cerabilia* s. str. species.
9. Elytral discal punctures- [0] none; [1] one; [2] two; [3] three; [4] greater than three. Having a single puncture in interval 3, situated at or slightly apical of

- the mid-length of the elytron and close to or touching stria 2 is the most common condition in Abacetini.
10. Elytral humeral angle- [0] relatively sharp, denticulate or with very prominent callosity if not sharp (from wear); [1] rounded, without denticle, at most a low bump or minute tooth. In the majority of Abacetini the humeral tooth is small, not well-developed, or absent. *Cerabilia* s. str. species are one of the few cases of an extremely large, sharp humeral tooth.
 11. Elytral plica- [0] absent; [1] small, internal ridge present, but not evident externally; [2] large, from short and wide to long and narrow, but always externally evident. A majority of Abacetini species have state 2, an evident plica, but it is absent in a great many species as well. A well-developed plica may have been derived and lost repeatedly in Carabidae (Liebherr 1986).
 12. Elytra setigerous punctures on intervals 5 and 7- [0] absent; [1] present. The series of setae in the outer elytral intervals are only found in a small number of *Oxycrepis* species, though similar patterns of setation are known to be common in various groups of Harpalini.
 13. Impression and extent of elytral striae- [0] clearly impressed, reaching or nearly reaching base; [1] not impressed in the basal 5th and often not impressed or very shallow except near apex. Short, shallowly impressed striae only found in some species of *Cerabilia* (Will 2020).
 14. Mesepisternum macrosculpture- [0] punctate; [1] smooth or very lightly scabridulous. See character 15 for discussion of terms.
 15. Mesosternum macrosculpture- [0] punctate; [1] smooth or very lightly scabridulous; [2] rugulose or scabridulous; [3] rugosissimus. The forms of ventral macrosculpture in *Cerabilia* requires the use of particular terms as introduced by Will (2020b): scabridulous- having a lightly impressed, rather irregular network or series of lines; rugulose- lines are deeper and more regularly parallel; rugose- still more deeply impressed at least in part, but there is variation in the depth and form; rugosissimus- very deep, dense, and parallel impressions, typically covering the entire sclerite when present.
 16. Mesothoracic paramedial carinae- [0] absent; [1] present.
 17. Metasternal medial longitudinal sulcus- [0] present, obvious and deeply impressed; [1] absent or scarcely impressed and difficult to see.
 18. Metasternal transverse sulcus extent laterally- [0] more than 1/3 mesocoxa width laterad medial margin of mesocoxa; [1] 1/3 or less mesocoxa width laterad medial margin of mesocoxa. The metasternal transverse sulcus is the external indication of the anterior edge of the katepisternum (Beutel 1992). There is some correlation with the sulcus length and flight ability. Full-winged species almost always have the sulcus extended far laterally and brachypterous species frequently having a very short sulcus. But there are cases where these vary independently.
 19. Metasternal transverse sulcus form- [0] straight; [1] angulate or arcuate.
 20. Metasternum anterior margin- [0] flush ventrally; [1] with constriction and declivous area.
 21. Metepimeron form- [0] elongate and rounded (Fig. 3C); [1] short and slightly rounded (Fig. 3E); [2] very short truncate, either rectangular or triangular (Fig. 3D, F).
 22. Metepisternum macrosculpture- [0] smooth or very lightly scabridulous; [1] rugulose or scabridulous; [2] rugosissimus; [3] shallowly punctate. See character 15 for explanation of sculpture terms.
 23. Microsculpture of dorsal surface of pronotum- [0] not apparent at 50×; [1] visible as isodiametric or irregular mesh of sculpticells; [2] visible as transversely elongate sculpticells.
 24. Microsculpture of elytra- [0] not evident at 50×; [1] visible as isodiametric or irregular mesh of sculpticells; [2] visible as transversely elongate sculpticells.
 25. Number of elytral intervals- [0] only nine apparent; [1] 10 intervals apparent, the tenth convex at least for part of its length. Interval 10 is usually only apparent in the apical half and tends to become obscure or narrowed near the elytral base. It is also often less convex than the other intervals.
 26. Proepisternal strigilatory file- [0] absent; [1] present. Only known from species of *Abacetus* (Darlington 1962).
 27. Proepisternum macrosculpture- [0] punctate; [1] smooth; [2] slightly, irregularly rugose; [3] rugosissimus. See character 15 for explanation of sculpture terms.
 28. Pronota form- [0] basally not constricted, lateral margins sinuate, arcuate, or straight; [1] basally constricted, lateral margins arcuate anterad basal constriction.
 29. Pronotal basal setae- [0] position at or very near the level of the basal margin; [1] located distinctly apical level of basal margin.
 30. Pronotal setae- [0] plurisetose, with more than 2 pairs of setae along the entire lateral margins; [1] two pairs of setae, being the seta at the hind angle and medial positions; [2] only the medial pair of setae present.
 31. Pronotum anterior submarginal sulcus- [0] complete, impressed across the entire width or at most with a very short, medial interruption in some individuals; [1] incomplete, not impressed in a large section medially; [2] absent, not impressed.
 32. Pronotum basal impressions- [0] clearly marked, sharp and linear; [1] marked by shallow depressions, linear or broader; [2] absent.
 33. Pronotum mediolateral seta position- [0] very near or touching margin, not more than 2× the setal pore width distant from marginal channel; [1] very distant from margin, clearly more than 2× than setal pore width distant from marginal channel. Character state 1 is only found in a few species of *Cerabilia* (*Biliacera*).
 34. Prosternal process form- [0] apex rounded or blunt; [1] apex truncate.

Table 1. Comparative summary of past and present classifications of loxandrine-series taxa.

Taxon	Moore, 1965	Allen & Ball, 1980	Allen, 1982	This study
<i>Aulacopodus</i>	Included	Included	Included	Not included, transferred to Pterostichini
<i>Cosmodiscus</i>	Included	Included	Removed	Not included, placed in Abacetini incertae sedis
<i>Tiferonia</i>	Not treated	Included	Included	Not included, placed in Abacetini incertae sedis
<i>Oxycrepis</i>	Not treated	Included	Included	Included
<i>Loxandrus</i>	Included	Included	Included	Included, restricted to New World taxa, subgenus of <i>Oxycrepis</i>
<i>Adrimus</i>	Not treated	Included	Included	Included, subgenus of <i>Oxycrepis</i>
<i>Stolonis</i>	Not treated	Included (as subgenus of <i>Oxycrepis</i>)	Included (as subgenus of <i>Oxycrepis</i>)	Included, subgenus of <i>Oxycrepis</i>
<i>Metoncidus</i>	Not treated	Included	Included	Included, subgenus of <i>Oxycrepis</i>
<i>Pediomorphus</i>	In <i>Abacetus</i> series	Not treated	Not treated	Included
<i>Zeodera</i>	Included	Included	Included	Included, expanded to include Australian and New Guinea taxa
<i>Haploferonia</i>	Not treated	Included	Included	Included, subgenus of <i>Zeodera</i>
<i>Nebrioferonia</i>	Not treated	Included	Included	Included, subgenus of <i>Zeodera</i>
<i>Homalonesiota</i>	Not treated	Not treated	Included	Included, subgenus of <i>Zeodera</i>
<i>Cerabilia</i>	Included (<i>Feronista</i> species only)	Included (<i>Feronista</i> species only)	Included (<i>Feronista</i> species only)	Included, three subgenera: <i>Cerabilia</i> s. str., <i>Feronista</i> and <i>Biliacera</i>

35. Prosternal process margin- [0] not bordered; [1] with raised border along apical margin.
36. Male protarsi- [0] symmetrically expanded; [1] asymmetrically expanded (Fig. 3A); [2] asymmetrical slightly expanded; [3] symmetrical and narrow (Fig. 3B).
37. Meso and metatibiae- [0] medium to lightly built and finely spined; [1] robust with heavy spines.
38. Mesocoxal anteriolateral setae- [0] one; [1] two; [2] three; [3] greater than 3; [4] none.
39. Metacoxal sulcus- [0] sinuate or arcuate; [1] straight and appressed to anterior margin.
40. Metacoxa macrosulpture- [0] smooth; [1] lightly, shallowly rugose; [2] clearly rugose.
41. Metatibiae- [0] straight or nearly so; [1] arcuate, especially in males.
42. Metatrochanter setae- [0] absent; [1] present.
43. Protibial antennal cleaner clip setae- [0] two; [1] four; [2] six.
44. Protibial anterior spur- [0] smooth edged; [1] serrulate edged. Character state 2 is restricted to some *Stolonis* (Will 2005; Anichtchenko and Will 2009) and *Adrimus* species. It is often difficult to score in small species with a very fine spur or due to wear and the general condition of the specimen. Serrulate spurs are not common in Carabidae, but are found on the metatibia of masoreines (Jeannel 1942a; Ball and Bousquet 2000).

Abdomen and genitalia

Ventrites are glabrous or rarely finely and sparsely pubescent and the sculpturing is smooth or slightly rugulose. Ventrites do not have deep foveate punctures nor transverse sulci. Ventrite 6 of males has two paramedial setae except in *Metoncidus*, which has four, and females have four setae except in a few *Oxycrepis* species with only two, e.g., *O. strigomeroides*.

Female reproductive tract

One of the most striking features of species of *Loxandrina* is the variation in the female reproductive tract. Species may have the typical, elongate spermatheca, such as is found in nearly all Pterostichini (e.g., Ortuño 1991, 1996; Bousquet 1999; Will 2002), have a very short spermatheca formed as a small pouch (Liebherr and Will 1998), lack a distinct spermatheca (Will and Liebherr 1997) or be more or less sclerotized (Will 2020b).

Male genitalia

The ostium of the median lobe is almost universally positioned dorsally and only rarely, and slightly, rotated laterally. The dorsal position of ostium of median lobe of the aedeagus is most likely plesiomorphic as it is the state of nearly all loxandrines. In those few taxa with a somewhat deflected ostium, the deviation is slight and not comparable to strongly contorted structures that are distinctly oriented to the left, as in many Northern Hemisphere Pterostichini, or to the right, as in various Australian Pterostichini (Moore 1965). The parameres are typically simple, somewhat conchoid, with left paramere larger than the right in species with the typical left side superior position in repose. The endophallus typically has specific structures such as variously developed sacs, spine fields and sclerotized regions. These features have been used with some success to differentiate closely related species and as potential synapomorphies (Allen 1972). In the genus *Oxycrepis*, some species of the subgenera *Adrimus*, *Stolonis* and *Oxycrepis* incertae sedis, the dorsal surface of the median lobe has a region of thin, translucent and almost membranous cuticle, such that the median lobe is only firmly sclerotized laterally in the apical portion of the blade. While the vast majority of *Oxycrepis* and *Zeodera* species have very simple male genitalia as described above, there is an extensive diversity of male genitalia found in the genus *Cerabilia*. In addition to

some *Cerabilia* species having the male genitalia rotated 180°, with the right side superior when in repose (Liebherr and Will 2015; Will 2020b), there are species with the dorsal ostium variously rotated laterally or covering a large portion of the median lobe blade. The endophallus in *Cerabilia* is highly variable and typically with very large spines. Although some species of Abacetina are known to have males with only a single testis (Will et al. 2005) all *Loxandrina* examined have two testes and well developed accessory glands.

Abdominal and genital characters and character states used in the phylogenetic analysis

45. Ventrite 6 in female- [0] with two setae; [1] four setae; [2] six setae; [3] more than six setae.
46. Pygidial gland efferent duct- [0] simple, unmodified; [1] with basal lobe. The presence of an efferent duct lobe (state 1) (Will et al. 2000: their fig. 9) may be correlated with formic acid and hydrocarbon production in the pygidial glands but chemical data is too poorly sampled across Abacetini to come to a conclusion at this time.
47. Aedeagus median lobe ventral surface- [0] completely sclerotized cuticle; [1] broadly membranous. Straneo (1991: 5) states that he found South American species to rarely have an aedeagus with a distinct external shape, “nearly or completely lacking and apical blade,” and “so little sclerotized that its shape is ill defined.” This is a curious contrast to work by Allen (1972) that was heavily focused on characters of the aedeagus, though primarily the structure of the endophallus. It appears that Straneo’s conclusion was based on a limited number of specimens that were frequently teneral and the custom of gluing genitalia to cards, which often results in distortion or shriveling of the median lobe. It is true that some *Oxycrepis* males have only a thin marginal and apical region of the aedeagus sclerotized (state 1) (Will 2005) but examination and storage in glycerine reveals that the apical blade is well-developed and distinctly shaped.
48. Aedeagus orientation in repose- [0] left side up; [1] right side up. The rotation of the male genitalia when in repose is most commonly left side up across carabids but there are several notable exceptions (Straneo 1942; Liebherr and Will 2015) all appear to be derived switches to right side up. Among all Abacetini the right side up condition (state 1) is found only in some species of New Caledonian *Cerabilia* (*Biliacera*).
49. Female reproductive tract bursa right dorsolateral sac- [0] absent; [1] present.
50. Female reproductive tract right dorsolateral sac form- [0] elongate horn-shaped or elongate with subapical expansion; [1] bursa-form; [2] absent; [3] diverticulate.
51. Female reproductive tract spermatheca form- [0] stalked on elongate duct; [1] elongate, horn-like; [2] short, broadly connected to oviduct; [3] short, small, sessile; [4] no obvious spermatheca.

Defensive chemicals of the pygidial glands

Salicylaldehyde was found to be the primary pygidial gland chemical in two Australia species of *Loxandrus* (Moore and Wallbank 1968) and was suggested as a synapomorphy for *Loxandrina* (Bousquet and Larochelle 1993) when those were the only species known for their gland products. Straneo (1991) was correct in pointing out that the sample was too limited to deem it as strong evidence for exclusion of *Loxandrina* from Pterostichini on its own. However, Straneo’s overall distrust for chemical evidence is probably incorrect. Will et al. (2000, 2001) found that seven species of *Oxycrepis* from North and South American all produced formic acid as a primary compound. The Australian species *Z. rufilabris* (Laporte, 1867) and *C. (Feronista) monteithi* (Baehr, 2007) were also found to produce formic acid and not salicylaldehyde (Will and Attygalle unpublished). It seems likely that salicylaldehyde is derived for only some Australian *Zeodera* and formic acid, which is also known from abacetines (Will and Attygalle unpublished and B.P. Moore in litt.) is plesiomorphic for the tribe.

Larvae

Larval characters have not been studied for many loxandrines or related taxa. Only *Oxycrepis velocipes* (Casey, 1918), *O. semperfidelis* (Will, 2008), and *O. oophaga* have described larvae (Bousquet 1985; Costa et al. 2011; Will 2008). I have reared loxandrine larvae from adults of 10 South American species (mix of described and undescribed species in *Oxycrepis incertae sedis* and *Stolonis*), one North American species (*O. icarus* (Will & Liebherr, 1997)) and one Australian species (*Z. longiformis* (Sloane, 1898)). All of these are very similar to *O. velocipes* and *O. semperfidelis*. The larva of *O. oophagus*, however, is very different from all others, being eruciform and glabrous (Costa et al. 2011), and preying on anuran eggs in their foam nest. Too few larvae are known to include larval characters in this analysis or even to speculate on the phylogenetic significance of any similarities or differences among abacetines.

Taxonomic results and accounts

Approach to generic and subgeneric classification.

Genus-group names are defined here to represent monophyletic groups as far as the available evidence allows and then nomenclatural precedence is followed

for generic and subgeneric names used. Shifting to an evidence-based classification consistent with the phylogeny requires recombining a large number of species previously included in *Loxandrus* in either *Zeodera* Laporte, 1867 or *Oxycrepis* Reiche, 1843. These two genera in their traditional, strict sense were monotypic (*Zeodera*) or included only four species (*Oxycrepis*), but given the new concept of the genera presented here, now include many dozens of species each (Fig. 1). The species included originally are distinct in general habitus from all other loxandrine taxa and it is perhaps a quirk of nomenclatural history that such highly characteristic taxa like these were described first in their respective faunas. No doubt for those people that have developed an understanding of the classification and identification of *Loxandrina* genera in its traditional arrangement it will be difficult to shift away from the at-a-glance recognition of the old concept of *Loxandrus* to the classification established here. This study shows that the apparently radical difference among the various extreme forms previously recognized as genera are derived from a form and suite of characters that are plesiomorphic and the intermediates are numerous and significant.

Classifications are most effective and have their greatest information content when they are consistent with the process that produced the pattern of relationships and diversity of the currently recognized biologically significant entities, i.e., monophyletic genera and species. The division of *Loxandrus* auctorum into two great clades that don't share a most recent common ancestor exclusive of *Pedimorphus* Chaudoir, 1878 and *Cerabilia* Laporte, 1867 is reflected in the nomenclatural changes as demanded by the Linnaean system now implemented by The Code (ICZN 1999). To continue to recognize many of the genera as distinct would imply a pattern of common ancestry and synapomorphy that is not realized by any character evidence and would obscure the biogeographical history of the group, particularly the old and significant splits between the New World and Australia.

Subgenera are retained and restricted to include only those species in this analysis or those that have been studied sufficiently and have explicit, published character evidence that can be used as a basis for inclusion. Many species that have not been adequately studied or documented are included as incertae sedis at the level for which evidence exists. For example, most species of Central and South American *Oxycrepis* have only brief descriptions and I have only made a cursory study of them. These are all placed as *Oxycrepis* incertae sedis given that they can only be placed in the large, New World clade and cannot be confidently assigned to the subgenus *Loxandrus* clade or the clade containing *Oxycrepis* s. str. A more complete analysis including all or many more of the New World species may be able to place all taxa. At that point the generic concepts may need further adjustment.

Taxa removed from *Loxandrina*

Tribe Pterostichini Bonelli, 1810

Genus *Aulacopodus* Britton, 1940

Type species. *Pterostichus sharpianus* Broun, 1893: 163, by original designation.

Selected literature. Keys and descriptions in papers by Britton (1940), Moore (1965), and Laroche and Larivière (2007, 2016).

Described species and range. Four species restricted to New Zealand.

Adult characteristics. Species are very typical looking pterostichines, similar to a medium sized unadorned species of *Notonomus* or *Pseudoceneus* Tschitschérine, 1901. All are reddish-brown to black, 8–12 mm in length, and brachypterous.

Life history notes. Laroche and Larivière (2007) list three of the four species as very hygrophilous and all are reported as forest dwelling species.

Discussion. Moore (1965: 9, in key) included this taxon in his loxandrine series and asserted that *Zeodera* “comes closest” to this genus. Based on couplet #35 in Moore's key, *Aulacopodus* species would have an “absent or vestigial” parascutellar striole. However, as stated by Britton (1940: 491), all species have the parascutellar stria “well marked” and the abs1 is present.” Subsequent authors have followed Moore's implied informal classification, but apparently without examination of specimens. Additionally, the metacoxal sulcus ends near the mid-line well short of the coxal apex, the male protarsi are expanded but not asymmetrical, and the right paramere in the male is narrow and blunt.

In general, *Aulacopodus* species are not particularly loxandrine-like. Specifically the truncate metacoxal sulcus and the abs1 are not known from any loxandrine species. All the other characters noted above are found in some loxandrine species but never in combination as in *Aulacopodus*. The combination of two or three setiferous punctures on elytral interval 3 and the short metacoxal sulcus is typical for *Setalis* series species (sensu Moore (1965)), which are part of the larger euchroine clade (Will 2000). However, the female reproductive tract in *Aulacopodus* is not the goose-neck form as typically found in Euchroines. *Aulacopodus* species have a cup-like bursa, with both the spermatheca and appended gland present, but no additional diverticulae. This form of female tract is typical of taxa attributed to the *Notonomus* series (sensu Moore (1965)). Unlike *Notonomus* series taxa the pygidial gland reservoirs of *Aulacopodus* species do not have a distinct dorsal lobe. Both *Aulacopodus* and *Pseudoceneus* have a narrowed right paramere in the male genitalia and lack the parascutellar setigerous puncture. *Aulacopodus* and *Pseudoceneus* are also otherwise so similar that they may prove to be synonymous. Analysis of DNA sequence data consistently places *Aulacopodus* and *Pseudoceneus* as sister taxa, with both of these allied with the *Notonomus* series taxa, and never close to any Abacetini taxa (Will 2015a, Will unpub.).

Tribe Abacetini Chaudoir, 1873**Abacetina****Genus *Cosmodiscus* Sloane, 1907**

Type species. *Cosmodiscus rubripictus* Sloane, 1907: 372, by monotypy.

Selected literature. Key to New Guinea species (Darlington 1962), discussion of systematics and description of new species (Straneo 1940, 1983).

Described species and range. Eight species that cover a range from India, to Japan, New Guinea, and Australia.

Adult characteristics. Species are medium to small sized, 5–9 mm, rather broad bodied beetles with very prominent eyes and sharply curved mandibles. In general they are reminiscent of some Drimostomatini taxa but do not share the characteristic rotated, right side up aedeagus found in that tribe (Straneo 1942).

Life history notes. In leaf-litter on the ground in New Guinea rainforests (Darlington 1962, p.514) and taken at mercury vapor lights (EMEC specimens).

Discussion. While *Cosmodiscus* is clearly within Abacetini there is no evidence that it is a member of *Loxandrina*. Moore (1965, p.9 in key) included this genus in the loxandrine series and this position was maintained by Allen and Ball (1980). Allen (1982, p. 403) removed the genus from the series based on a “preliminary study” but did not discuss his evidence for this decision or suggest an alternative placement. In Straneo’s (1940, 1983) discussion on the systematic position of *Cosmodiscus* he notes that the only character of distinction separating this genus from *Aristopus* LaFerté-Sénéctère, 1853 is the lack of the dorsal elytral setigerous puncture such as is found in all *Aristopus* species. He concludes that *Cosmodiscus* is allied with *Aristopus* and those two genera with *Metaxys* Chaudoir, 1857 and *Cyrtomoscelis* Chaudoir, 1874. Based on my study of these genera, *Cosmodiscus* probably is congeneric with *Aristopus* but a formal synonymy cannot be established until a comprehensive review the genera of Abacetina is done for these taxa and other African and Oriental region groups, e.g., *Inkosa* Péringuey, 1926, *Metabacetus*, *Mateuellus* Deuve, 1990. All of these genera are very likely closely related within Abacetini.

Genus *Tiferonia* Darlington, 1962

Type species. *Tiferonia parva* Darlington, 1962: 562, by original designation.

Selected literature. Review of genus and key to species (Will 2020a).

Described species and range. Four species from New Guinea, the Philippines, Cambodia (B. Gueorguiev in litt.), and central Africa.

Adult characteristics. Small sized beetles (3.5–5.0 mm). These beetles are moderately convex, shiny, brown and the elytra somewhat or significantly irides-

cent. In general form they are similar to some small species of *Lecanomerus* Chaudoir, 1850 or larger *Tachys* Dejean, 1821. Recognizable from other, similar looking abacetine genera by the combination of deep post-ocular sulcus, smooth elytral margins; and lack of elytral discal setae.

Life history notes. Wet, shady areas near water (Darlington 1962).

Discussion. Darlington described *Tiferonia* as being “a minute *Loxandrus*” with a few significant differences, he also discusses the possibility that they are related to *Melanchrous* Andrewes or *Holconotus* Schmidt-Goebel, 1846 (= *Fouquetius* Maindron, 1906), with the latter relationship having more character support. *Tiferonia* has sinuate metacoxal sulci that end in the middle of the coxa, sharply impressed and divergent frontal impressions, symmetrically expanded male protarsi, a moderately transverse mentum, and lacks the puncture on interval 3 of the elytral disc. All of these characteristic are also found in *Holconotus*, but also in many other Abacetina taxa. *Tiferonia* and *Holconotus* species share the presence of a sharply impressed sulcus on the non-ommatidia portion of the ocular orbit just behind the eye, a character not found in any other Abacetini species and likely a synapomorphy for these two genera. *Tiferonia* lacks the serrulations near the humeri on the elytral marginal bead that are found in *Holconotus* species (Will 2020a). *Tiferonia* does not have the asymmetrically inserted second antennomeres as is found in *Abacetus* and many other putatively related genera. Given its character state combination, *Tiferonia* is most likely in a grade of Abacetina taxa, near genera like *Metabacetus* and *Cosmodiscus*.

Taxa included in *Loxandrina*

All presently described species of *Loxandrina* are placed in recognized genera, subgenera, or as incertae sedis (Suppl. material 1). The classification changes created eight secondary homonyms that are resolved as follows: *Oxycrepis gebi*, replacement name for *O. balli* (Straneo, 1993); *O. amatona*, replacement name for *O. matoana* (Straneo, 1993); *O. xiproma*, replacement name for *O. proxima* (Straneo, 1993); *O. rasutulis*, replacement name for *O. suturalis* (Straneo, 1993); *O. laevinota*, replacement name for *O. laevicollis* (Bates, 1871); *O. arvulap*, replacement name for *O. parvula* (Straneo, 1951); *O. noaffine*, replacement name for *O. affinis* (Straneo, 1991); *O. alutona*, replacement name for *O. notula* (Tschitschérine, 1901).

Subtribe *Loxandrina* Erwin & Sims, 1984

Type genus. *Loxandrus* LeConte, 1853: 250. Type species *Feronia recta* Say 1823: 58, by subsequent designation (Casey 1918).

Genus *Oxycrepis* Reiche, 1843

Type species. *Oxycrepis leucocera* Reiche, 1843: 78, by monotypy.

Subgenus *Loxandrus* LeConte, 1853; type species *Feronia recta* Say, 1823: 58, designated by Casey (1918).

=*Megalostylus* Chaudoir, 1842 nec Schoenherr, 1840; type species *Feronia recta* Say, 1823 designated by Casey (1918: 325)

Subgenus *Adrimus* Bates, 1872; type species *Loxandrus viridescens* Bates, 1871: 132, designated by Straneo (1977).

Subgenus *Metoncidus* Bates, 1871; type species *Metoncidus tenebrioides* Bates, 1871: 134, by monotypy.

Subgenus *Stolonis* Motschulsky, 1866; type species *Stolonis notula* Motschulsky, 1866: 231, by monotypy.
= *Prostolonis* Mateu, 1976; type species *Prostolonis martinezi* Mateu, 1976, by original designation. Synonymy by Allen and Ball (1980: 527)

Selected literature. Review of some South American species (Straneo 1991, 1993), treatments of North American species (Allen 1972; Bousquet 2006), synopsis of Mexican species (Allen and Ball 1980), new South American species (Will and Liebherr 1997; Will 2004, 2008; Anichtchenko and Will 2009; Costa et al. 2011).

Described species and range. Currently 244 species are described. The vast majority of species are found in tropical South America. The group extends south to at least southern Buenos Aires Province, Argentina, north through tropical South America, Central America, the Caribbean and eastern North America as far north as Ontario, Canada, in the southwest west to Arizona, USA and east to the Atlantic coast.

Adult morphology. The most diverse genus in *Loxandrina*. Though most *Oxycrepis* species are very similar looking, with a body form generally similar to an average platynine or small pterostichine, the genus includes several highly divergent forms that have been described and recognized as genera. The most common form is well represented by, *O. recta* the type species of the subgenus *Loxandrus* (Fig. 4), which contrasts with species that have the pronotum decidedly narrow throughout, with the width equal to or less than the length, or very narrowly constricted at the base (*Oxycrepis* s. str., *Stolonis* (Figs 6, 7)) and the distinctly parallel-sided forms (*Metoncidus* (Fig. 8)). A few species described in *Adrimus* and *Loxandrus* have a distinctive, relatively short, broad pronotum and more oval elytra with very large eyes (Fig. 5) (Will and Liebherr 1997). *Oxycrepis* species range from small to medium size (3.2–15 mm). Most are black or piceous and some are castaneous or brown. Legs, mouthparts and the ventral surface of the body may be paler than the dorsal surface and legs are frequently strongly contrasting paler, flavous or orangish brown. In some species the distal or medial antennomeres are white and strongly con-

trasting with other, black or heavily infuscated antennomeres. In many species the elytra have variously arranged pale spots or vittae, paler first elytral intervals or a more or less well-defined paler region at the apex of the elytra (Fig. 6). Many are glossy and very often have a more or less prominent spectral iridescence. A smaller number are matt from a deeply impressed mesh microsculpture (e.g., *O. opacula* (Bates, 1871) and *O. sculptilis* (Bates, 1884)). The majority of species appear to have large and functional flight wings and flight to lights at night has been commonly observed. But significant reduction of the flight wings is known across the genus. The apex of the prosternal process is smooth and a raised margin, like what is common in *Zeodera*, is very rare, only known from one described species, *Oxycrepis mirei* (Straneo, 1991). The elytral plica is typically well-developed, but is often very small and narrow, or absent as in the species Allen and Ball (1980) assigned to the *infimus* group. Most species have a single discal puncture in the elytral interval 3 but *Metoncidus*, *Stolonis* and *Oxycrepis* s. str. frequently have additional elytral setae. Males of many species have notably asymmetrically expanded protarsomeres but unmodified or only subtly expanded protarsomeres occur in a few species from across the genus.

Life history notes. These beetles are terrestrial, epigeal, usually found in moist to very wet habitats. They may be associated with standing or running water, though species in Central and South American rainforests can frequently be found far from water in very wet, closed canopy forests. They are nocturnally active, generalist predators that are frequently found in mixed species aggregations. I have collected as many as six species together under a single rock in localities in southeastern USA. Tropical species are frequently found at high density in areas with fallen flower-petals and/or fruits (Paarmann et al. 2002, 2001; Will unpublished data).

Discussion. Nominally seven genus-level taxa are subsumed in this clade. Of those, *Megalostylus* is a junior homonym of *Megalostylus* Schoenherr, 1840 (Curculionidae) and *Prostolonis* is currently considered a junior synonym of *Stolonis*. The other five have been considered generically distinct, but *Oxycrepis* s. str., *Adrimus*, *Stolonis* and *Metoncidus* are all derived from within a clade of New World species that were classified as *Loxandrus* by previous authors. This renders a concept of *Loxandrus* that includes all the New World species paraphyletic (Fig. 1). North American species that are included in the analysis form a clade sister to the remaining species, which appears consistent with recognition of *Loxandrus* s. str. as a genus. However, currently there is no satisfactory way to separate *Oxycrepis* (*Loxandrus*) species from *Oxycrepis* incertae sedis (see key, couplet 16). Given that many species cannot be confidently assigned to either the subgenus *Loxandrus* clade or the clade containing *Oxycrepis* s. str., the appropriate level to apply the genus based on evidence is the clade including the entire set of New World species. Therefore, *Adrimus*, *Stolonis*, *Metoncidus* and *Loxandrus* are herein treated as subgenera. Of the five genus-level taxa included, *Oxycrepis* has nomenclatural priority.

Allen (1972) revised most of the taxa in what is now the subgenus *Loxandrus* and this early effort was then further refined and expanded by Allen and Ball (1980) and then by Bousquet (2006). Bousquet defined nine species groups and provided character states for each. While the monophyly of these informal groups were not broadly tested, six of nine were included in the present study, three represented by more than one species; *agilis* group, *celeris* group, and *erratica* group. All of those groups were found to be monophyletic with high support (PP 1.0) and form a clade with the species representing the *saphyrina* and *recta* groups.

The species of these five groups are all included in the subgenus *Loxandrus*. They are all similar in general form and share a combination of character states. They are typically medium sized (5–13 mm), black or piceous, with legs, antennae, and mouthparts often paler, flavous or orangish brown. Elytra are uniformly dark or rarely have an orange spot near the apex. Many are somewhat or very glossy and have an obvious spectral iridescence, especially ventrally. The majority of species appear to have large and functional flight wings, but rarely the flight wings are reduced. Elytral interval 3 has a single puncture and the elytral plica is well-developed. Males have distinctly asymmetrically expanded protarsomeres. The metepisternum is long and apically rounded. The apex of the prosternal process does not have a raised margin. The mentum tooth does not reach the level of apices of lateral lobes and the paramedial pits are indistinct.

The subgenus *Adrimus* was initially established as a genus by Bates (1872) to include *Loxandrus* auct. species that have a very short, parallel-sided metepimeron. Bates also noted for those species where he had male specimens, that unlike species he included in *Loxandrus*, the protarsomeres were only slightly expanded and symmetrical. Straneo (1993) briefly discussed the taxonomic position of *Adrimus* and described 11 additional species. Straneo reiterated that the *Adrimus* species have males with symmetrically expanded protarsomeres (Fig. 3B) and the metepimeron “very short and truncate at the apex” (Fig. 3D). I have examined types or authoritatively identified specimens (CMNH, MCSN, MNHN, EMEC) of all but six of the 23 species attributed to *Adrimus* and found that they vary in both of these characters. Four forms of the metepimeron are present among these species (Fig. 3C–F; character 21): 1. Long, rounded, typical form in *Oxycrepis* (*O. latibasis* (Straneo, 1993)); 2. Short rounded apex (*O. elytralis* (Straneo, 1993)); 3. Very short parallel-sided, truncate (corresponding to descriptions of Bates and Straneo) in *O. aenescens* (Tschitschérine, 1900), *O. affinis* (Tschitschérine, 1900), *O. gebi* Will, *O. fuscipes* (Brullé, 1835), *O. longior* (Straneo, 1993), *O. xiproma* Will, *O. rasutulis* Will, *O. uruguaica* (Tschitschérine, 1903), *O. ventralis* (Straneo, 1993), *O. rufangula* (Bates, 1872), and *O. viridescens* (Bates, 1871); and 4. Short, triangular (*O. claripes* (Straneo, 1993), *O. iridea* (Straneo, 1993), *O. amatona* Will, *O. paulensis* (Straneo, 1993).

Five *Adrimus* species are known only from the female holotype and for five others I have not examined males. Among the species I have examined male protarsomeres have three forms (Fig. 3A–B; character 36): 1. symmetrical and slightly expanded (*O. crepera* (Bates, 1872), *O. fuscipes*, *O. gebi*, *O. iridea*, *O. microdera* (Bates, 1872), *O. rasutulis*); 2. asymmetrical expanded, typical form as found in many typical *Oxycrepis* (*O. affinis*, *O. longior*, *O. uruguaicus*, *O. ventralis*); and 3. symmetrical and very narrowly expanded (*O. viridescens*, *O. claripes*, *O. amatona*).

There is no clear correlation of the states for the characters of the male protarsi and metepimeron. *Oxycrepis* (*A.*) *viridescens* was selected by Straneo (1977) as the type species for *Adrimus*. This species has both the very short, parallel-sided, truncate metepimera and symmetrical, slightly expanded male protarsomeres.

Unfortunately specimens of *Adrimus*-like species are rarely collected. I included only two species in my analysis from which I could extract DNA, one from Brazil and one from Colombia. Both are typical *Adrimus* in that they have a very short, truncate metepimeron. As these two are found to be most closely related to each other with very high support (PP 1.0, Fig. 1), and nest well within the *Oxycrepis* clade, *Adrimus* is treated as subgenus. As a working hypothesis, those species with any of the three short metepimeron states and those species not yet examined for the state of the metepimeron are included in the subgenus. As *O. (A.) latibasis* (Straneo, 1993) has a long rounded metepimeron it is moved to *Oxycrepis* incertae sedis.

Allen and Ball (1980) considered *Oxycrepis* s. str. as a close relative of *Stolonis* but recognized the four species included in *Oxycrepis* s. str. as a distinctive group of relatively large sized, hirsute species having an elongate-ovoid pronotal form. This is consistent with subsequent studies (Will 2005) and the results found here, which place *Oxycrepis* s. str. sister to *Stolonis* including an undescribed *Oxycrepis* species that has some features of Straneo’s species group-17 (Straneo 1991), such as bi-colored antennae. Only *O. cordata* Tschitschérine, 1900 was included in the current analysis, but I have also examined types or confidently identified material for *O. leucocera* Reiche, 1843 and *O. brasiliensis* Tschitschérine, 1900, which share the same form, patterns of setation, and most character states with *O. cordata* (Will 2005).

Stolonis species are typically recognized by their narrowly constricted pronotal base and serrulate protibial spurs. This subgenus appears to be monophyletic but there is a great deal of variation and overlap in some characters with other *Oxycrepis*. *Stolonis* includes some species with bi-colored antennae and legs, states also found in *Oxycrepis* s. str. and Straneo’s group-17 species. A few *Stolonis* species have additional setae on elytral intervals 3, 5, and 7, such as is found in species of *Metoncidus*. Some species have the dorsal surface of the median lobe with a region of thin, translucent and almost membranous cuticle similar to what is found in some species of *Adrimus*. There is variation in pronotal shape, but all are notably basally narrowed, most are more or less prolonged be-

yond the level of the hind setae (Will 2005). Until a more detailed study of the included species and their respective types is done, species described in *Stolonis* are retained in the subgenus.

Metoncidus is a small, exclusively South American subgenus that includes three species with a distinctive combination of character states including an elongate, parallel-sided form, relatively short antennae, male ventrite VI with four setae, and many setae on elytral intervals 3, 5, and 7. The species were recently treated (Will 2004). Of the three species, only *O. (M.) epiphytes* was included in the analysis and this species was placed in a derived clade of South American *Oxycrepis*.

More than 150 species are placed in *Oxycrepis* incertae sedis. Informal groups of species that have been created in previous works are used to help organize these taxa by some notion of similarity (Suppl. material 1), but formal subgeneric classification based on synapomorphies will require detailed revisionary study.

Genus *Pedimorphus* Chaudoir, 1878

Type species. *Pedimorphus planiusculus* Chaudoir, 1878: 29, by monotypy.

Selected literature. Review of genus, key to species and synonymies (Will 2010, 2015b, 2019).

Described species and range. Thirteen species all restricted to Australia.

Adult morphology. Species of *Pedimorphus* are small, 3.5–8.2 mm (most around 4.5 mm), dorsoventrally depressed, usually pale, flavous or castaneous, usually with crenulate elytral stria. All species have enlarged labial palpomeres with a setose, ventral sensorium, subocular carina, evident elytral plica, and lack elytral discal setae.

Life history notes. *Pedimorphus* are commonly taken at lights at night and are known from open habitats (Moore 1965), under cow dung and at the edge of swamp (Sloane 1900), and I have found them under mats of dead grass along a flooded ditch (Will 2019).

Discussion. The species included form a well-supported clade sister to *Zeodera*. In addition to DNA sequence data for the exemplars, the modified palps and derived lack of dorsal puncture on the elytra found in all species are synapomorphies.

Genus *Zeodera* Laporte, 1867

= *Poeciloidia* Tschitschérine, 1891. Type species *Feronia iridescens* Laporte, 1867: 132 (sensu Tschitschérine, see Straneo (1937), Moore (1965) and Moore et al. (1987))

Types species. *Zeodera atra* Laporte, 1867: 114, by monotypy.

Subgenus *Haploferonia* Darlington, 1962

Type species. *Haploferonia simplex* Darlington, 1962: 548, by monotypy.

Subgenus *Homalonesiota* Maindrón, 1908

Type species. *Homalonesiota karawarii* Maindrón, 1908: 295, by monotypy.

Subgenus *Nebrioferonia* Straneo, 1939

Type species. *Nebrioferonia strigitarsis* Straneo, 1939: 119, by monotypy.

Selected literature. Keys to genus-level taxa (Moore 1965; Baehr and Will 2019), treatment of New Guinea taxa (Darlington 1962, 1971; Allen 1982), descriptions and key to some Australian taxa (Sloane 1903).

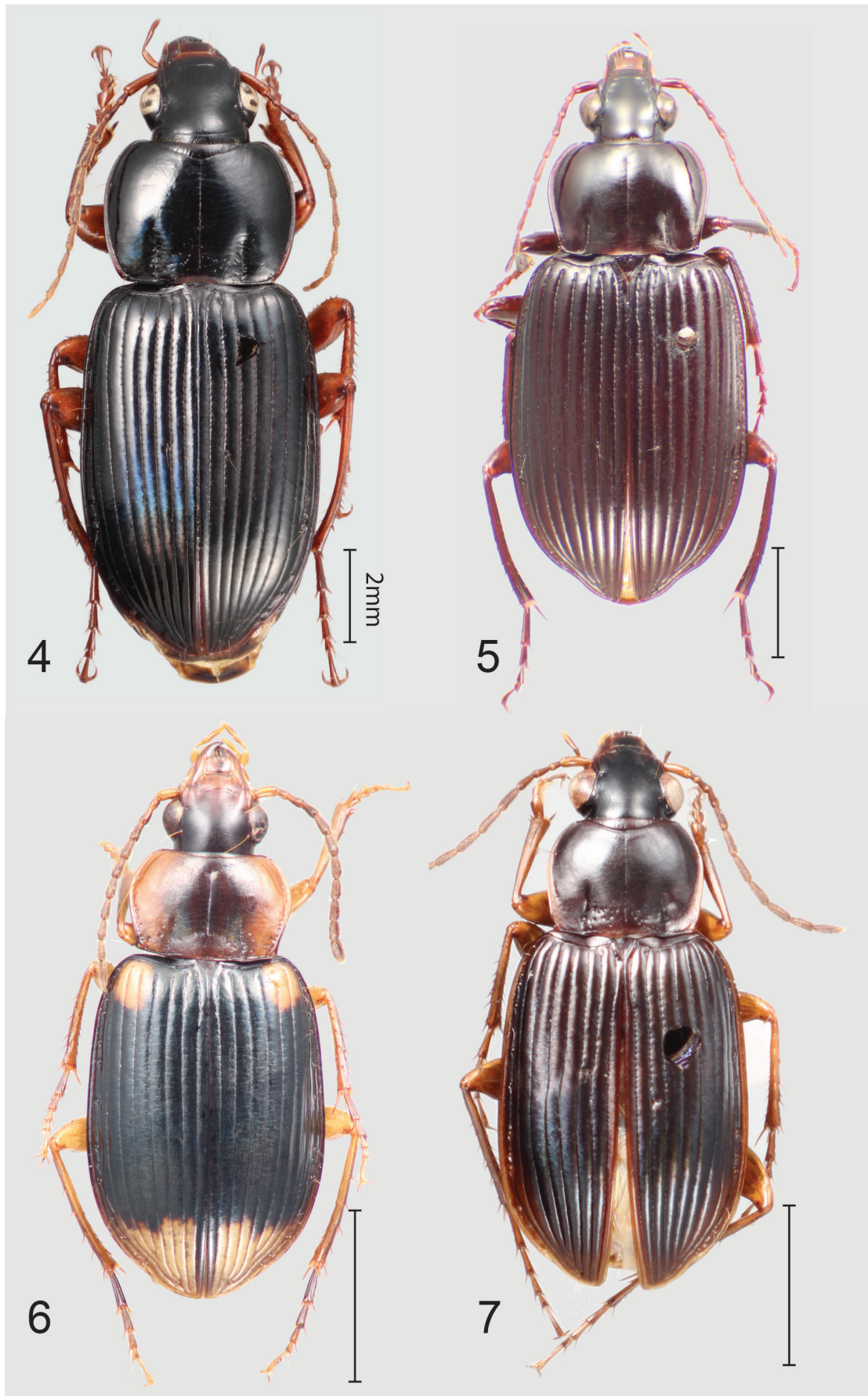
Described species and range. Twenty five species are presently described from Australia, New Guinea and Sulawesi.

Adult characteristics. Medium to moderately large sized beetles (6.0–22.0 mm). Most are black or piceous and some are castaneous or brown. Legs, mouthparts and the ventral surface of the body may be paler than the dorsal surface, but not more than moderately contrasting. The elytra are concolorous and never have distinct pale spots or vittae; at most the elytron may be slightly paler on the first interval and vaguely paler near the apices of the elytra. Many are very glossy and often with a more or less prominent spectral iridescence. Species from the drier interior of Australia are frequently a dull matt from the prominent mesh microsculpture. The apex of the prosternal process has a raised margin in the majority of species. The elytral plica varies from large and well-developed to completely absent. Elytral interval 3 consistently has a single discal puncture. Though most species are very typical looking *Loxandrina* and so reminiscent of platynines in general body form, the genus also includes forms from very broad, *Abax*-form as in *Z. atra*, (Fig. 13) to broadly ovoid in *Z. lata* (Fig. 16), and narrow-elongate in *Z. longiformis*.

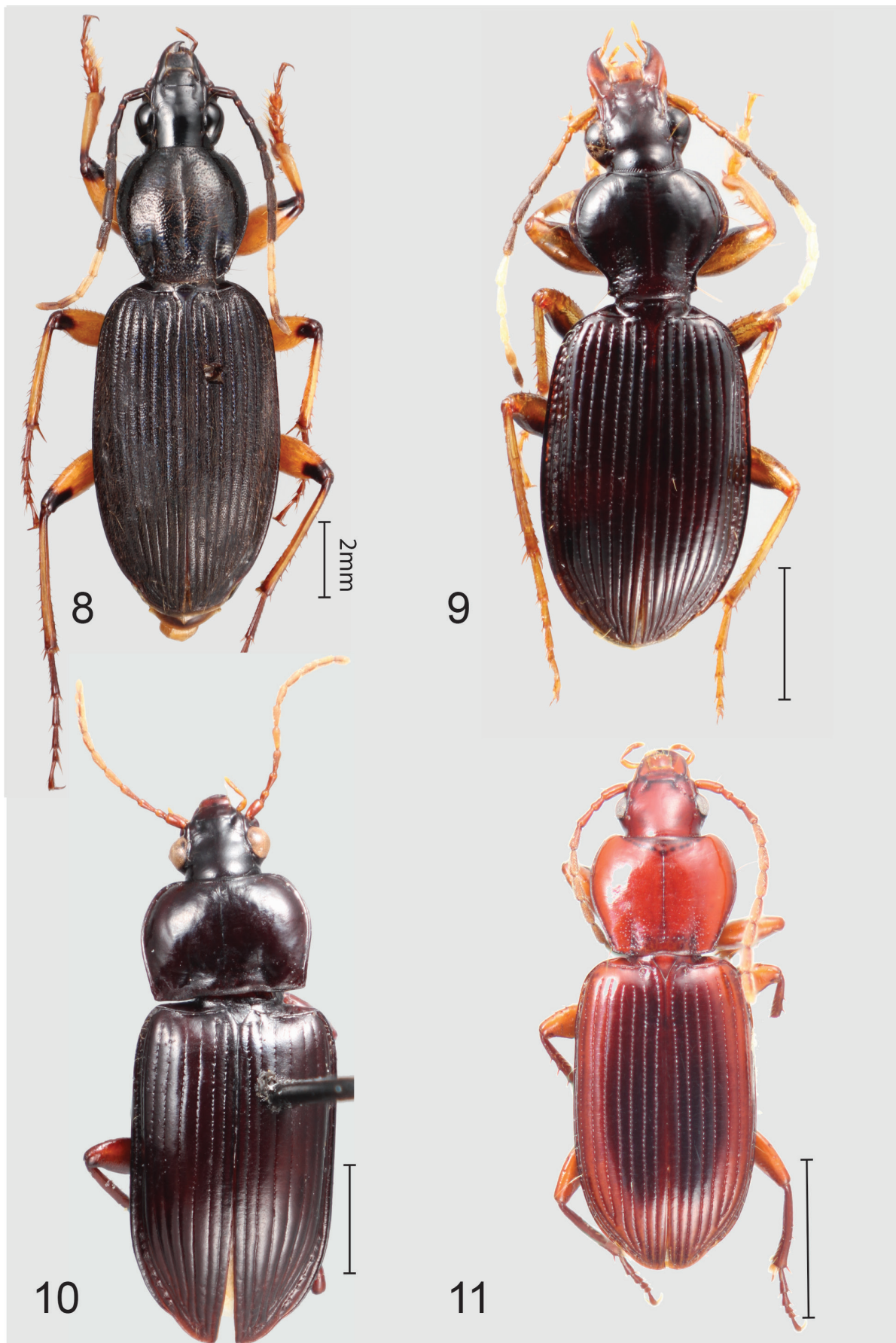
Larvae. No larval descriptions have been published for any *Zeodera* species. I have examined a larva of *Z. longiformis* (reared by B.P. Moore). It is a typical looking loxandrine larva, similar to the described larvae of *O. velocipes*.

Life history notes. Species of *Zeodera* are found across habitats from rainforest (uncommonly), closed forests (Moore et al. 1987), to a wide variety of more open habitat types near permanent and seasonal, lentic and lotic water in arid regions. They are generally very hygrophilous with some species found in stream and river gravel and cobble directly over running water. By far the greatest diversity and abundance of *Zeodera* is encountered in backwater areas along oxbows, billabongs, near seasonal lakes, in riparian flood areas, and in wet roadside ditches. Typically they are abundant in muddy places with abundant leaf litter flotsam, or tangles of matted grasses. They are nocturnally active and those that fly can be very abundant at lights. A few species are found in open grassland with no apparent surface water (Guthrie et al. 2010).

Discussion. There are five genus-level taxa that were recognized by previous authors that are included in the *Zeodera* clade: *Loxandrus*, which is herein restricted to New World taxa, *Zeodera*, *Homalonesiota*, *Nebrioferonia*, and *Haploferonia*. *Zeodera* has priority as the earliest estab-



Figures 4–7. Habitus. 4. *Oxycrepis (Loxandrus) recta* (Say); 5. *O. strigomerooides* (Straneo); 6. *O. elnae* (Allen); 7. *O. (Adrimus) rasutulis* Will.



Figures 8–11. Habitus. **8.** *Oxycrepis* (s. str.) *cordata* (Tschitschérine); **9.** *O. (Stolonis) tapiai* (Will); **10.** *O. (Metoncidus) epiphyta* (Will) (holotype); **11.** *Pedimorphus planiusculus* Chaudoir.

lished genus-level taxon among the four names for taxa in the clade. Darlington (1962) repeatedly noted (as did Allen (1982)) that these genus-level taxa are scarcely different from *Loxandrus* auct. and proposed that they were derived from that stock and are part of a closely related group in the Australian and New Guinea region. The results of this study confirm Darlington's intuition. Exemplars included in the analysis for all of these taxa nest within the broader *Zeodera* clade. To reflect the phylogeny these genus-level taxa are now treated as subgenera of *Zeodera*.

The four subgenera were all originally established as genera based on overall body shape and a small number of morphological features that in combination distinguish them (see the key). The nominate subgenus of *Zeodera* only includes *Z. atra*, which has a distinctive broad body form, short metepisternum and evident elytral interval 10. *Zeodera (Haploferonia) simplex* (Fig. 14) also has a short metepisternum and evident elytral interval 10, but has a more typical elongate body form. Additionally, *Z. simplex* lacks the elytral plica that is very well developed in *Zeodera atra* and most species of *Zeodera*. The presence of the partial interval 10 of the elytra appears independently in various species, including other abacetines such as *Cerabilia*, *Cyrtomoscelis*, and outside abacetines in similarly flightless pterostichines such as *Lesticus* Dejean, 1828, *Rhytiferonia* Darlington, 1962, *Rhabdotus* Chaudoir, 1865, and *Parhypates* Motschulsky, 1866. The short metepisternum in both of these species is consistent with a change in the thorax after losing the ability to fly. *Zeodera atra* is well-known as a rainforest species (Moore 1965; Moore et al. 1987) and is not restricted to near water areas. Likewise, *Z. simplex* is relatively large, flightless, and presumed to be a rainforest species (Darlington 1962). These species appear to occupy a similar ecological role as the comparable-sized and often flightless *Prosopogmus* and *Lesticus* species also found in the region. Other rainforest *Loxandrina*, such as all Australian and New Caledonian *Cerabilia* and many Neotropical *Oxycrepis*, are small to minute with various flight wing development.

While *Z. simplex* is placed within the *Zeodera* clade its relationship to other species remains uncertain. It is only known from the single female holotype and the character data available for analysis is very limited. Darlington (1962) described the "scutellar striae" of *Z. simplex* as "absent or nearly so", but then later refers to them as simply absent (pg. 548). The basis for this confusion seems to be that there are very small, slightly impressed marks on each elytron of the holotype in a position almost corresponding to the angular base of stria 1. However, the marks are much too close to the midline and base of the elytron to truly correspond to the angular base of stria 1. Developmental aberrations of this type are known, but rare, in various South American *Oxycrepis* (Will 2008). When present the impressions are short, or may appear as a nearly fully developed angular base of stria 1 but always only unilaterally or unequally if there is any indication on both sides. The elytral marks in *Haploferonia* are not interpreted as indicating the presence of the angular base of

stria 1. Since only one specimen is known for this species, the true extent of variation for this character is unknown.

Homalonesiota (Fig. 17) and *Nebrioferonia* (Fig. 15) were treated as closely related by Allen (1982) with the configuration of the sulci of the tarsomeres and setae on the mesocoxa given as synapomorphies. I did not find support for a sister-group relationship and there appears to be some confusion regarding morphological character states for these species. Initially Straneo (1939) described *Nebrioferonia* to include the single species *N. strigitarsis*. Subsequently, Darlington (1962) described a second species, *N. straneo*, that he later (Darlington 1971) transferred to *Homalonesiota* placing it together with Maindron's *H. karawarii*. An additional species, *N. intermedia* was then described by Allen (1982). In his paper, Allen attempted to clarify apomorphic and synapomorphic characteristics to substantiate the genus-level taxa. He proposed that *Nebrioferonia* and *Homalonesiota* share synapomorphic state of having quadri-sulcate meso- and metatarsomeres 1–4 and a trisetose mesocoxa. I have examined more than a dozen specimens of species from each of these subgenera, including paratypes for *Z. (Homalonesiota) straneo* and *Z. (Nebrioferonia) strigitarsis* and the holotype and paratype of *Z. (Nebrioferonia) intermedia*, and found that *Homalonesiota* specimens constantly have only one anteriolateral and one posteromedial mesocoxae setae (bisetose) and *Nebrioferonia* constantly have two anteriolateral and one posteromedial mesocoxal setae (trisetose) counter to what is reported by Allen (1982) that all of these species were trisetose. A trisetose mesocoxa (Character 38) is constant in *Nebrioferonia*, and there are scattered occurrences across carabids of apparently fixed multiple mesocoxal anteriolateral setae, for example in some *Calathus* Bonelli, 1810 species (Schmidt and Will 2020), but this state is otherwise only known from loxandrine species that are polymorphic for mesocoxal setae number (*O. cordata* and *O. semperfidelis*).

Darlington (1962) states that "The first 3 segments of the middle and hind tarsi are 4-sulcate (5-costate) above in *N. strigitarsis*; broadly 2-sulcate (3-costate) in *N. straneo*". He again confirms this difference in his description of *H. straneo* and redescription of *H. karawarii* Maindron (Darlington 1971). However, Allen (1982) enumerates the characteristics of *Nebrioferonia*, including quadri-sulcate tarsi, and then adds "These characters also apply to the genus *Homalonesiota*." In his discussion of character states and proposed phylogenetic relationships, quadri-sulcate tarsomeres are considered synapomorphic for *Nebrioferonia* and *Homalonesiota*. I have examined specimens of both species of *Nebrioferonia* and *Homalonesiota straneo* and find that Darlington's description of the tarsi is correct.

Aside from the trisetose mesocoxae in *Nebrioferonia* and the notably elongate antennomere 1 in *Homalonesiota*, there is no significant difference between these species and other *Zeodera* species. There is also no clear evidence that these taxa form a clade within *Zeodera*. The New Guinea *Zeodera* species are scattered across the clade suggesting that there are multiple connections, possibly dispersal events, between Australia and New Guinea.

Genus *Cerabilia* Laporte, 1867

- = *Nelidus* Chaudoir, 1878; type species *Nelidus australis* Chaudoir, 1878: 50, by monotypy. Synonymy by Will (2015b)
- = *Zabronothus* Broun, 1893; type species *Zabronothus striatulus* Broun, 1893: 1327, designation by Laroche and Larivière (2001). Synonymy by Laroche and Larivière (2007)
- = *Australomasoreus* Baehr, 2007; type species *Australomasoreus montethi* Baehr, 2007: 6, by original designation. Synonymy by Will (2015b)

Type species. *Cerabilia maori* Laporte, 1867: 116, by monotypy. Republished description Laporte, 1868: 202. Subgenus *Feronista* Moore, 1965; type species *Feronista amaroides* Moore, 1965: 26, by original designation. Subgenus *Biliacera* Will, 2020; type species *Cerabilia vitalis* Will, 2020:79, by original designation.

Selected literature. Revision, keys to species, generic descriptions, and synonymies for Australian and New Caledonian taxa (Moore 1965; Will 2011, 2015b, 2020b). For New Zealand taxa see publications by Laroche and Larivière (2001, 2007, 2016).

Described species and range. Sixty-one species described from northeastern Australia (30 spp.), New Zealand (7 spp.), and New Caledonia (24 spp.).

Adult characteristics. Very small to medium sized beetles (3.4–11 mm), slightly to significantly broader and more convex than typical for taxa in the subtribe. At one extreme of the body forms *Cerabilia* species are nearly as oval and convex as a typical *Cosmodiscus* and on the other extreme, they are elongate ovoid, approaching the typical *Zeodera* body form. Easily recognizable among loxandrines by

combination of the very short metepisternum, completely reduced flight wing, heavily built legs with robust spines, and absence of the elytral plica. Among *Zeodera*, only *Z. lata* (Darlington) (Fig. 16), a flight-wing dimorphic species from New Guinea, is somewhat similar to the broad-body form typical of *Cerabilia*. However, *Z. lata* lacks several of the character states listed above that are found in *Cerabilia*.

Life history notes. All species are found in rich leaf litter of wet forests and rainforests. They are difficult to find during the day, but are readily collected at night in forest leaf litter. It appears that they are in the upper soil layer during the day and emerge during the night. They are uncommonly found under rocks or woody debris in the forest.

Discussion. The phylogeny presented here includes less than half of the described species of *Cerabilia* but it shows strong support for the monophyly of the genus in the combined analysis (PP 0.99), however, analyses of sequence data alone does not include a *Cerabilia* clade. The monophyly of the New Caledonian subgenus *Biliacera* is well supported in all analyses and very strongly (PP 1.0) in the combined data analysis. The exclusively Australian subgenus *Feronista* is supported as a clade in combined analysis, but with modest support (PP 0.63). In both combined and sequence data only analyses all species of *Feronista* are found to comprise a clade except for *Cerabilia (F.) oodiformis*, which is sister to the *Biliacera* clade but with modest support (PP 0.70). *Cerabilia* s. str. is only represented in the analyses by two species and while the pair always emerges as sister species, their position as sister to *Feronista* only has modest support (PP 0.64) in the combined analysis and in the sequence data only analysis they are sister to the *Cerabilia (F.) oodiformis* + *Biliacera* clade.

Identification of Abacetini and Loxandrina

A variety of Harpalinae taxa are superficially similar to members of Abacetini. Typically abacetines will run to Pterostichini, or the equivalent supertribal or subfamilial taxon in regional keys. A combination of character states, most of which are the absence of identifying features of other tribes, can be used to identify a specimen as a member of Abacetini.

Readily observable anatomical features typically used for identification are variable in Loxandrina, this requires running some of the taxa out at multiple points in the key. In addition to character states, distributional information is a very useful guide to a correct identification.

- 1 Harpalinae with the presence of *any one or more* of the following character states: angular base of stria 1 present (Fig. 2A–C); truncate elytral apex; moniliform antennae; mouth parts with many very long stiff setae; lack of obvious suture medially between mentum and submentum; abdominal ventrites with deep punctures in a transverse row or impressed transverse sulci; tarsal claws pectinate; prominent metallic color; or single supraorbital setae (among Abacetini single supraorbital setae only known in *Tiferonia brunnea* and *Abacaecus waltherrossii*). See discussion above.)..... other pterostichine grade or Pterostichini-like Harpalinae taxa, consult regional keys if available.
- Without *any* of the characteristics above. Abacetini..... 2
- 2 Presence of *any one or more* of the following character states: Antennomere 2 prominently asymmetrically inserted onto 1; metacoxal sulcus arcuate, sinuate and/or ending well before lateral apex; mentum extremely short and transverse or proepisternum with stridulatory file or pegs. In addition the elytral plica is usually present and male protarsomeres symmetrically expanded. Distributed throughout Africa to southern Europe, tropical and subtropical Asia south to Australia (Fig. 21)..... Abacetina
- Without *any* of the characteristics above, except for the elytral plica, which may be present or absent and male protarsomeres, which may be broadly, asymmetrically expanded, symmetrically expanded or narrow (Fig. 3). Distributed between the low, temperate latitudes of North and South America and the Australian region (Fig. 21)..... Loxandrina

Key to genera and subgenera of *Loxandrina*

- 1 Dorsal surface of pronotum and elytra entirely hirsute..... *Oxycrepis* (s. str.) (Fig. 8) [South America]
 – Dorsal surface of pronotum glabrous and elytra glabrous, usually with a single setigerous puncture in interval 3. Rarely without the setigerous puncture or with a few fixed elongate setae in interval 3 or in all odd numbered elytral intervals..... 2
- 2(1) Elytral interval 3 without setigerous punctures..... 3
 – Elytral interval 3 with one or more setigerous puncture..... 6
- 3(2) Labial apical palpomere fusiform or acuminate, lacking a ventral sensorium. Body somewhat or very convex..... 4
 – Labial apical palpomere subglobose with a ventral sensorium. Body somewhat or distinctly flat *Pediomorphus* (Fig. 11) [Australia]
- 4(3) Elytral humeral angle with prominent, sharp denticle..... 5
 – Elytral humeral angle rounded, without denticle..... *Cerabilia* (*Feronista*) (Fig. 19) [Australia]
- 5(4) Distinctly oodine-like body form. Parascutellar puncture present. Elytral striae shallowly impressed apically and not impressed in basal 5th *Cerabilia* (*Feronista*) *oodiformis* [Australia]
 – Elongate ovoid body form. Parascutellar puncture present or absent. Elytral striae impressed to or nearly to base....
 *Cerabilia* (s. str.) in part (Fig. 18) [New Zealand]
- 6(2) Pronotum with lateral margins straight, sinuate or rounded to the base, but width never very narrowly constricted to the base. Level of the pronotal basal margin at or very nearly at the same level as the baso-lateral setae..... 7
 – Pronotum cordiform, very distinctly narrowed basally. Basal margin at a level produced well beyond the level of the baso-lateral setae in most species *Oxycrepis* (*Stolonis*) (Fig. 9) [South America north to southern North America]
- 7(6) Metepimeron elongate or somewhat short but rounded apically (Fig. 3C, E) 8
 – Metepimeron very short, rectangular or narrowly triangular and truncate apically (Fig. 3D, F).....
 *Oxycrepis* (*Adrimus*) (Fig. 7) [South America]
- 8(7) Elytral interval 3 with two, one, or no setigerous punctures in apical half or third 9
 – Elytral interval 3 with five to ten setigerous punctures in apical half or third.....
 *Oxycrepis* (*Metoncidus*) (Fig. 10) [South America]
- 9(8) Pronotum without posteriolateral seta. Elytral interval 3 with one to five setigerous punctures..... 10
 – Pronotum with posteriolateral seta. Elytral interval 3 with only one setigerous puncture. 11
- 10(9) Elytra with evident plica. Elytral interval 3 with one setigerous puncture. *Zeodera lata* (Fig. 16) [New Guinea]
 – Elytra without evident plica. Elytral interval 3 with one to five setigerous punctures
 *Cerabilia* (*Biliacera*) (Fig. 20) [New Caledonia]
- 11(9:) Antennomere 1 equal or shorter than 2 and 3 combined..... 12
 – Antennomere 1 longer than 2 and 3 combined..... *Zeodera* (*Homalonesiota*) (Fig. 17) [New Guinea]
- 12(11) Mesocoxae with two setae, one lateral and one posteriomedial..... 13
 – Mesocoxae with three setae, two lateral and one posteriomedial. *Zeodera* (*Nebriofonia*) (Fig. 15) [New Guinea]
- 13(12) Prosternal process without raised marginal border at apex. 14
 – Prosternal process with raised marginal border at apex. *Zeodera*, in part [Australia, New Guinea and Sulawesi].
- 14(13) Elongate, parallel-sided or ovoid body form. Flight wing and pronotal form variable. Medium to small size, rarely over 12 mm..... 15
 – Broad, *Abax*-like body form. Flight wing reduced. Pronotum trapezoidal. Large size, 16–22 mm
 *Zeodera* (s. str.) *atra* (Fig. 13) [Australia]
- 15(14) Lacking *one or more* of the features below. Typically black iridescent (maculate elytra in many New World species), moderately depressed body form, elytra usually with plica and normally full flight wing..... 16
 – With the following combinations of features: convex body form, concolorous brown, flight wing reduced, elytra without plica, elytral humeral angle with prominent, sharp denticle..... *Cerabilia* (s. str.) in part (Fig. 18) [New Zealand]
- 16(15) Distributed in Australia, New Guinea and Sulawesi. Raised marginal bead of the prosternal process usually present. ... 17
 – Distributed in North, Central and South America. Raised marginal bead of the prosternal process usually absent
 *Oxycrepis* (*Loxandrus*) or *Oxycrepis* *incertae sedis*, in part
- 17(16) With the following combinations of features: metasternum medial sulcus not apparent. Elytra without plica, flight wing reduced, body form elongate, and pronotum elongate rectangular ... *Zeodera* (*Haploferonia*) *simplex* (Fig. 14) [New Guinea]
 – Lacking *one or more* of the features above. Metasternum medial sulcus apparent, often deeply impressed; elytra with evident plica, and full flight wing. Body form various *Zeodera*, in part (Fig. 12) [Australia, New Guinea and Sulawesi]

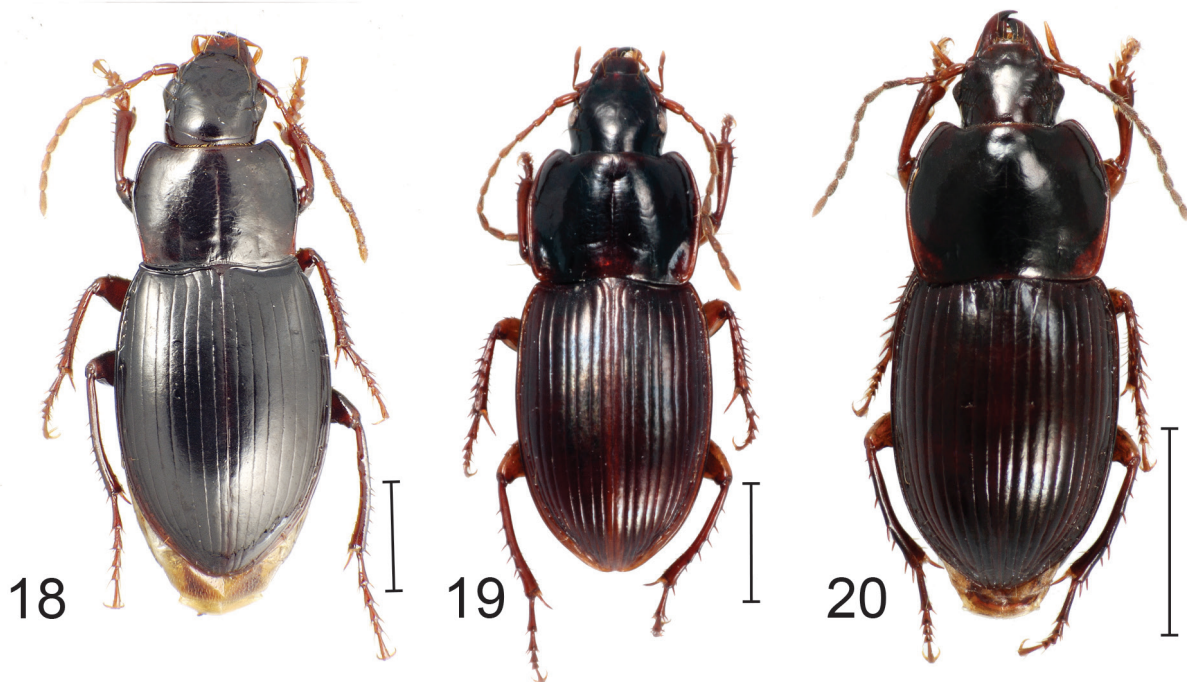
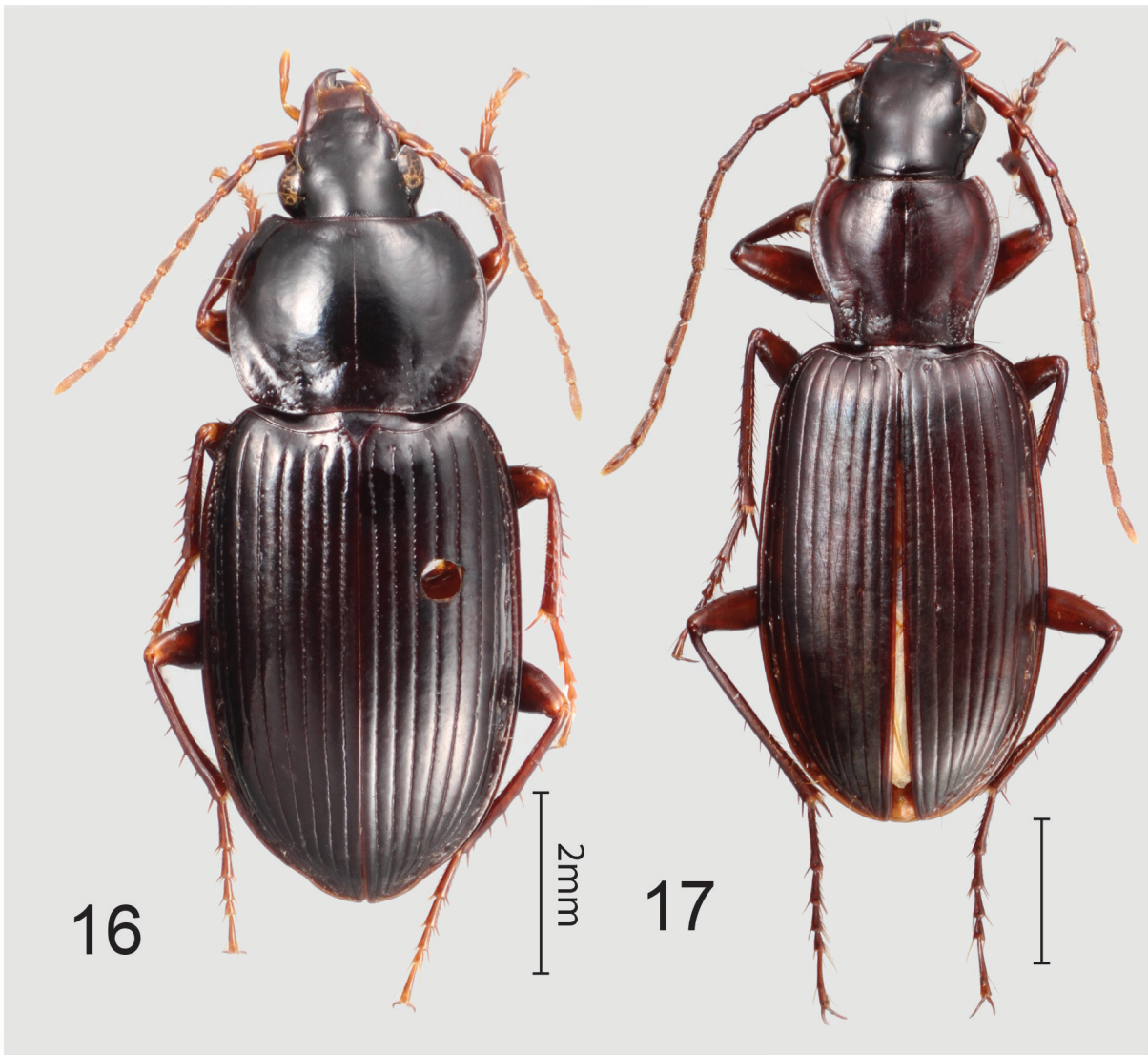
Historical biogeography

There is no fossil record for Abacetini. Without the means to confidently, temporally calibrate the phylogeny, test-

ing historical biogeographic scenarios for the group is severely limited (Donoghue and Moore 2003). However, a descriptive approach, constrained by the *Loxandrina* phylogeny and comparing the major patterns of spe-



Figures 12–15. Habitus. **12.** *Zeodera australiensis* (Sloane); **13.** *Z. (s. str.) atra* Laporte; **14.** *Z. (Haploferonia) simplex* (Darlington) (holotype); **15.** *Z. (Nebrioferonia) strigitaris* (Straneo).



Figures 16–20. Habitus. **16.** *Zeodera lata* (Darlington); **17.** *Z. (Homalonesiota) straneoi* (Darlington); **18.** *Cerabilia* (s. str.) *striatula* (Broun); **19.** *C. (Feronista) storeyi* Will; **20.** *C. (Biliacera) klingonorum* Will.

cies distributions and relationships with the sequence of well-supported geological events as a framework for hypotheses of the timing of vicariance and diversification can be a good starting point. Such scenarios are advanced with the assumption that long-distance dispersal and massive, rapid extinctions have happened infrequently enough that the pattern in the known, extant taxa is a good representation of the events of the past. One must also give significant weight to geological evidence while being mindful that those are also hypotheses of historical events and that the subaerial landscape the beetles now inhabit is the result of a complex history of accretion, submergence, reemergence, exposure to an ever-shifting climate, and major changes in dominant habitats (Allen and Ball 1980; Mcloughlin 2001).

Past historical biogeographic inferences for abacetines (Darlington 1971; Allen 1972; Allen and Ball 1980) are only partially comparable to the present study given the dramatic differences in taxa included (Table 1). However, the “Australian-American discontinuity” (Darlington 1971: 229) of loxandrines is a disjunct pattern that has been noted by these prior studies and is specifically addressed here.

Darlington (1971) relied heavily, almost exclusively, on dispersal, extinction, and ecological correlates to develop his hypotheses of biogeographical history. From his view, loxandrines would have once occurred across the Old World tropics and dispersed to Australia by way of Asia. Once in Australia the Old World tropical groups would have gone extinct and subsequently Australian loxandrines re-disperse north into New Guinea and Sulawesi.

Allen (1972) proposed a fairly specific phylogeny-based biogeographical scenario for taxa that were at the time included in *Loxandrus* with a focus on the North and Central American species. The taxon sampling and phylogenetic methods available to Allen were not able to correctly resolve relationships among *Loxandrina* as a whole, placing various Australian taxa within New World taxa. Allen pointed out that problems he saw related to the Australian taxa that were included in his study, noting that “[i]t would be much simpler if it were possible to account for the Australian *Loxandrus* fauna being derived from a single phylogenetic line.” To Allen’s credit, he took the evidence he had at face value and proposed biogeographical and phylogenetic scenarios that were consistent with that. His intuition to the contrary – that the American and Australian taxa are separate lineages – has now been shown to be correct. Aside from some of the *Zeodera* species included in Allen’s study forming a clade based on the presence of the marginal bead of the prosternal process, a character state shared by nearly all *Zeodera*, there is no commonality between his results and the tree presented here for Australian taxa.

Allen and Ball (1980) then suggested that the Australian *Loxandrus* auct. were monophyletic and closely related to other Australian taxa, but no explicit evidence was presented to support this since their focus was on the Neotropical taxa. Unlike Darlington, Allen and Ball recognized that plate tectonics and vicariance could more simply explain disjunction than Darlington’s dispersal

and extinction model, and they postulated an origin of loxandrines in the “late Mesozoic time” with a trans-Antarctic distribution for the loxandrine “ancestral stock.” In broad strokes, Allen and Ball were correct regarding both phylogeny and biogeography.

The distribution of the tribe as a whole can be described as Gondwanan and amphi-Atlantic (“transatlantic (south)” and “amphiantarctic” of Erwin (1985) or “inabresia” (Jeanne 1942b; Reichardt 1977)). Numerous *Abacetina* genera are currently distributed throughout the African continent and across Asia, primarily in the tropics, while *Loxandrina* is entirely restricted to the Americas and the Australian region. The sister group of *Loxandrina* is not known, but it is most likely among the African or possibly Indian abacetines. In either case, the timing of the amphi-Atlantic split between the descendent lineages leading to *Loxandrina* and its sister group would correspond to the splitting of the African and Indian landmasses from the rest of Gondwana, sometime in the late Jurassic to mid-Cretaceous, approximately 105–165 Ma. The opening of the southern Atlantic involved a protracted, south to north splitting of Africa and South America, which leads to the later date that takes into account the time until the persistent contact or close proximity of the land masses in the north was fully separated. Given the Gondwanan and amphi-Atlantic distribution of *Abacetini* and the Australian-American disjunct distribution of *Loxandrina*, there are two plausible scenarios that may account for the present distributions. I refer to these as the southern origin and the northern origin scenarios.

The southern origin scenario

There is significant evidence that during the late Jurassic to mid-Cretaceous period an extensive belt of warm, humid climate, at middle to high latitudes, extended over southern South America, southern Africa, India, Australia and Antarctica (Hay and Floegel 2012). This warm, humid belt had a distinctive flora (Mcloughlin 2001) including temperate rainforests (Klages et al. 2020). At the same time, due to the super-continent effect, the equatorial and low-latitude region was a relatively hot and largely an arid zone, with the only possible area of year-round rainfall being the western edge of West Gondwana (Hay and Floegel 2012). An equatorial humid belt is not thought to have developed until around 100 Ma by which time the splitting of Africa and India from rest of Gondwana would have been complete, at least in the southern latitudes, and the *Loxandrina* lineage would have then been fully separated from the remaining *Abacetini*. It is likely that the arid zone across subtropical and tropical latitudes in northern West Gondwana was a barrier to *Abacetini* taxa in Africa and South America that prevented their northward extension into the developing equatorial humid belt. Such a barrier would explain why these landmasses, which were relatively closely adjacent, if not fully connected in the north at the time, do not share any *Loxandrina* or *Abacetina* taxa now, even though both continents have extensive humid tropics.

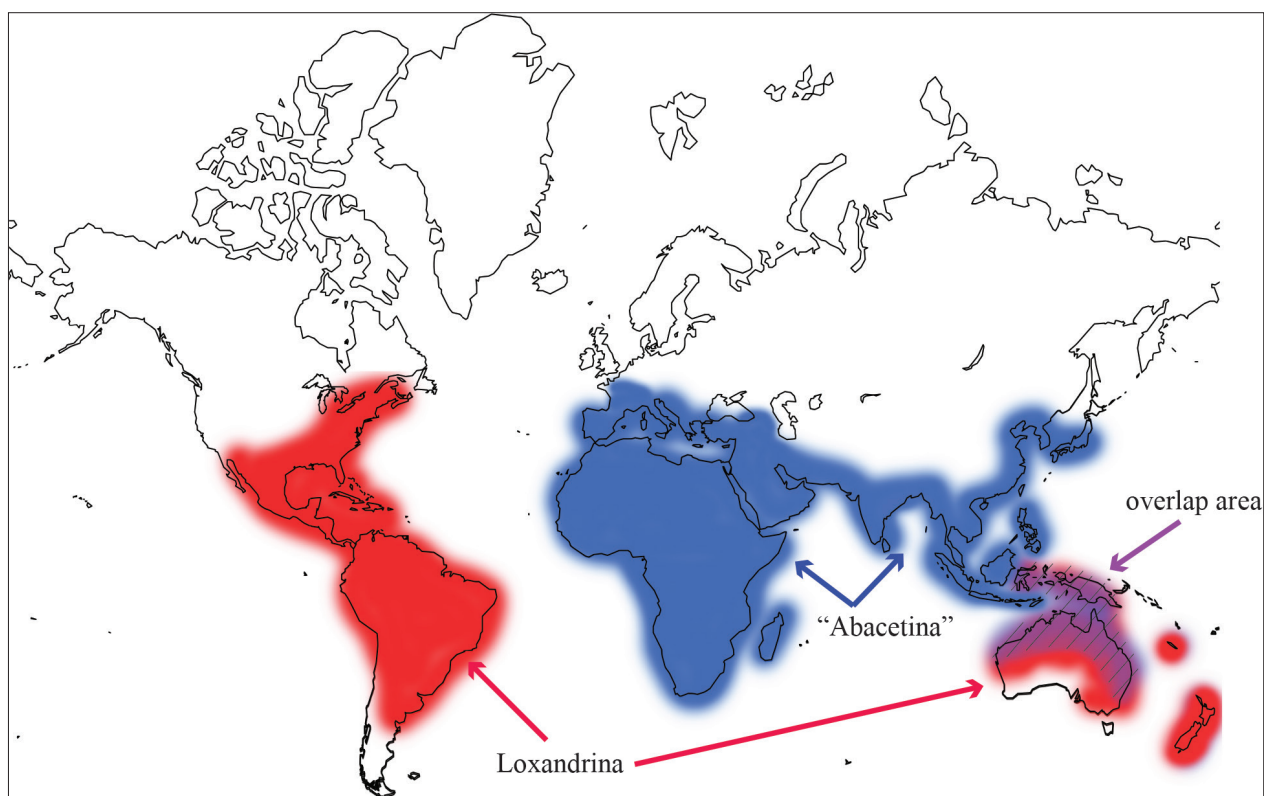


Figure 21. Generalized map of the distribution of Abacetini.

Loxandrina is split into two clades, *Oxycrepis* species are presently found in the Neotropical and Nearctic regions and the clade of *Zeodera*, *Pedimorphus*, and *Cerabilia*, are now exclusively in the Australian region. Assuming a southern origin, the common ancestor of these clades would have most likely had a trans-Antarctic distribution. The separation of the Australian and American lineages is certain to have been complete by 30 Ma, when the Australian and South American continents are thought to be fully separated from Antarctica. However, it is quite possible that the vicariance was much earlier. Between oldest possible time of the last common ancestor of Loxandrina and its sister group around 165 Ma and the full isolation of Antarctica 30 Ma, ending in the opening of the Tasman Gateway that created the Southern Ocean, several major events occurred. Any one of these events could have precipitated the disjunction. These events include the K-Pg extinction event 66 Ma (Renne et al. 2013), the cool shift in climate starting with the early opening of Drakes Passage at 40–50 Ma (Livermore et al. 2005), the barrier between Australia and Antarctica created by the widening Australo-Antarctic Gulf that opened west to east starting from at least 96 Ma (Boger 2011; Direen 2012), and two of the recognized climatic optima; early optimum around 50–55 Ma and middle around 40 Ma (McGowran and Hill 2015). A more detailed and time-calibrated phylogeny is needed to test for possible correspondence between these events and the distribution and diversification of loxandrine taxa or to consider the likelihood of any plausible, long distance dispersal events.

The northern origin scenario

In addition to the source area difference, there is an age difference between the two scenarios corresponding to the likely date of the split of the Abacetini common ancestor across the developing Atlantic. Unlike the southern origin above, under the northern origin scenario Abacetini was in the tropics at around 100 Ma when the equatorial humid zone developed in northern South America and northern Africa and not in the trans-Antarctic region until much later. The northern South America and northern Africa landmasses were still connected or relatively close at the time and one abacetine lineage was in or dispersed to South America and subsequently was separated from the African Abacetina lineages. This scenario was proposed for Galeritini (Ball 1985) and would also fit the amphi-Atlantic connections hypothesized for *Barylaus* Liebherr (Liebherr 1986). However, unlike those groups, the South American vicariant lineage of loxandrines diversified in the New World wet tropics and then would have moved south, across South America entering the warm and humid trans-Antarctica zone, and extended its distribution to Australia. The formation of the Southern Ocean and related changes in climate and habitat would mark most recent date for the resulting Australian-American disjunct distribution.

Under either the northern or southern scenario, loxandrines from South America were able to enter North America, possibly as early as the mid-Tertiary (Erwin 1979; Allen and Ball 1980), by way of an island arc be-

tween Central and South America (Cody et al. 2010) and then coincidentally with other animal and plant groups at the closing of the Isthmus of Panama around 3.5 Ma. Allen and Ball (1980) proposed up to eight “invasions” of Central and North America exclusive of *Stolonis*, though they thought this was likely to be an overestimate (Allen and Ball 1980: 568). The phylogeny presented here (Fig. 1) includes only three lineages entering Central and North America; subgenus *Loxandrus*, *sculptilis*-group, and *elnae*-group. Additionally, *Stolonis* is found across Central America and into southern North America.

The occurrence of *Cerabilia*, but not *Zeodera* or *Pediomorphus*, in New Caledonia and New Zealand could be due to an old, trans-Antarctic distribution and vicariance (Liebherr et al. 2011), consistent with the southern origin of *Loxandrina*, or more recent dispersal events, which are required if the notion that these land masses were largely or completely submerged until the Oligocene (Murienne et al. 2005; Grandcolas et al. 2008) is correct. While *Cerabilia* (*Feronista*) is now restricted to rainforest remnants in eastern Australia, *Zeodera* is widespread across Australia and north to Sulawesi. The scattering of New Guinea species across the *Zeodera* clade is consistent with Darlington’s (1971) suggestion that there have been several dispersal events into New Guinea and north west to Sulawesi by this group.

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Supplementary material 1

Loxandrina new classification

Authors: K.Will

Data type: species list

Explanation note: Checklist of all species included in *Loxandrina*.

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Link: <https://doi.org/10.3897/dez.67.55985.suppl1>

Supplementary material 2

Table of GenBank numbers

Authors: K.Will

Data type: Genbank Number

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Link: <https://doi.org/10.3897/dez.67.55985.suppl2>

Supplementary material 3

Tree figures for MrBayes and TNT analyses

Authors: K.Will

Data type: phylogeny

Explanation note: Tree figures file for Mr Bayes and TNT analyses. Two MrBayes trees for all data 80 OTUs and sequence data only 80 OTUS. Consensus tree from TNT analysis.

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Link: <https://doi.org/10.3897/dez.67.55985.suppl3>

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