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***Araucaria* beetles worldwide: evolution and host adaptations of a multi-genus phytophagous guild of disjunct Gondwana-derived biogeographic occurrence**

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### **Abstract**

*Araucaria* trees occur widely disjunct in the biogeographic regions Oceania and Neotropis. Of the associated entomofauna phytophagous beetles (Coleoptera) of various taxonomic groups adapted their life history to this ancient host tree. This occurred either already before the late Gondwanian interruption of the previously joint *Araucaria* distribution or only later in the already geographically separated populations. A bibliographic survey of the eastern and western coleopterans recorded on *Araucaria* trees resulted in well over 200 species belonging to 17 families. These studies include records of beetles living on 12 of the 19 extant *Araucaria* species. Their occurrence and adaptations to the host trees are discussed under aspects of evolution and co-speciation.

**Keywords:** *Araucaria*, Coleoptera, synopsis, evolution, co-speciation, South America, Oceania

## Zusammenfassung

Araukarienbäume kommen in den disjunkten biogeographischen Regionen Ozeanien und Neotropis vor. Von der mit diesen Bäumen vergesellschafteten Entomofauna haben sich phytophage Käfer (Coleoptera) unterschiedlicher taxonomischer Gruppen in ihrer Lebensweise an diese altertümlichen Bäume angepasst. Diese Anpassungen entstanden entweder vor der Aufspaltung der ehemals zusammenhängenden gondwanischen Araukarienvorkommen oder erst in den bereits geographisch voneinander getrennten Populationen. Bei einer Erhebung der östlichen und westlichen Araukarienkäfer konnten deutlich mehr als 200 Arten aus 17 Familien registriert werden. In diese Studie wurden 12 der 19 rezenten Araukarienarten mit einbezogen. Das Vorkommen dieser Käfer und die jeweiligen Anpassungen an ihre Wirtsbäume werden unter evolutionsbiologischen Aspekten diskutiert.

**Stichworte:** *Araucaria*, Coleoptera, Synopse, Evolution, Co-Speziation, Südamerika, Ozeanien

## Resumo

As araucárias ocorrem nas disjuntas regiões biogeográficas da Oceânia e Neotrópica. Da entomofauna associada à estas árvores estão besouros (Coleóptera) fitófagos de vários grupos taxonómicos que se adaptaram a estes hospedeiros antigos. Estas adaptações ocorreram antes da interrupção do antigo supercontinente Gondwana quando as araucárias ainda estavam localizadas numa área contígua ou, depois nas populações geograficamente separadas. A análise bibliográfica dos coleópteros relatados das araucárias revelou bem mais do que 200 espécies de 17 famílias. Estes estudos incluíram citações de coleópteros associados às 12 das 19 espécies do gênero *Araucaria*. A ocorrência e as adaptações aos hospedeiros estão sendo discutidas em relação à evolução e à co-especiação.

**Palavras chave:** *Araucaria*, Coleóptera, sinopse, evolução, co-especiação, América do Sul, Oceânia

## **Introduction**

According to fossil records, the origin of the primitive tree genus *Araucaria* (Araucariaceae) was in the late Triassic, about 220 million years ago, and these trees are considered the oldest extant conifers. In the beginning of the Jurassic, about 180 million years ago, the disintegration of the megacontinent Gondwana began. The former contiguous distribution of *Araucaria* trees became disjunct when 100 million years ago, the break-up was completed and South America, Africa and Oceania were separated. Today, the 19 still existing *Araucaria* species are restricted to tropical and subtropical regions of the Southern Hemisphere and occur mostly in highly diverse mountain rain forests. The natural distribution of these trees is limited to Oceania and the Neotropics: *Araucaria bidwillii* and *A. cunninghamii* in Australia, *A. cunninghamii* and *A. hunsteinii* in Papua New Guinea, *A. heterophylla* at Norfolk Island, *A. bernieri*, *A. biramulata*, *A. columnaris*, *A. humboldtensis*, *A. laubenfelsii*, *A. luxurians*, *A. montana*, *A. nemorosa*, *A. muelleri*, *A. rulei*, *A. schmidii*, *A. scopulorum* and *A. subulata* in New Caledonia, *A. araucana* in Chile and Argentina and *A. angustifolia* in Brazil and Argentina (Golte 1993, Kindel 2001). This biogeographic occurrence at the former extreme eastern and western margins of the Gondwana continent suggests that in the central regions all the *Araucaria* populations became extinct. The absence of Araucariaceae in Africa supports this assumption. Regional climatic conditions during the late Jurassic and Cretaceous ages probably lead to the disappearance of *Araucaria* trees in most parts of their original areas.

Both the high geological age and the disjunct distribution predestinate *Araucaria* trees and their inhabiting insects for evolutionary studies on insect-plant relationships. Today, we know several insect groups restricted in their occurrence to recent Araucariaceae. They belong to various taxa like the leaf beetle subfamily Palophaginae (Megalopodidae), the weevil tribes Araucariini (Cossoninae, Curculionidae) and Mecomacerini (Rhinorhynchinae, Nemonychidae) and the bark beetle genera *Hylurdreconus* Schedl, 1938, *Hylurgonotus* Schedl, 1951, *Pachycotes* Sharp, 1877 and *Xylechinosomus* Schedl, 1963 (Scolytinae, Curculionidae) (Kuschel 1966, 1994, Kuschel & May 1996, Mecke 2000, Wood 1986).

The question is if insect-*Araucaria* associations already existed before the splitting of Gondwana, and whether they are up to now recognizable in the extant populations. How evolved these insects after the separation of their biogeographical regions? Which insects colonized *Araucaria* trees later on in the disjunct areas?

To answer these questions a detailed overview of the entomofauna associated with *Araucaria* trees in South America and Oceania is required. In a first approach, we surveyed the insects inhabiting 12 of the 19 extant *Araucaria* species. The results are presented here. In a second approach, we studied adaptations of the Araucariofauna to the specific microhabitats provided by their host trees. These interorganismic relations have to be evaluated in order to understand the proximate links between an insect and its particular *Araucaria* host. Knowledge of the life history is needed for an interpretation of the ultimate factors leading to assumed co-speciations in particular of phytophagous insects and their host plants.

## **Material and Methods**

The data for this study were obtained from collections and completed by a bibliographic survey. Field studies were conducted 1997 to 2003 in southern Brazil, 2001 in New Zealand and 2002 in the southern Province of New Caledonia. At the latter location previously no detailed study on insects living on *Araucaria* trees had been undertaken. We collected the beetles from dead trunks and branches of *Araucaria columnaris* at Bourail, Baie de Tortues, Ile des Pins and La Foa, *A. laubenfelsii* at Mont Do, *A. montana*

at Mont Kaala, *A. muelleri* at Montagne des Sources and Goro Plateau and *A. rulei* at Col de Poro (Figs 1 – 6). Emerging adults were obtained in photoelectors (emergence traps) consisting of perforated plastic barrels (45 cm height, diameter 35 cm), sealed against light with a dark synthetic textile, and provided with a collecting box on top. The electors were filled with branches and logs, moistened every 1 – 3 days and emerging insects were removed weekly. Similar sampling was carried out in Brazil and results have been published in earlier papers (Mecke et al 2000, 2001).

In addition, a detailed literature search of *Araucaria*-associated insects was carried out. Kindly communicated personally records of Roger A. Beaver (Thailand), Pierre Jolivet (France), Michael Schneider (Mozambique) and Simon Lawson (Australia) were included.



Fig. 1: *Araucaria muelleri* on ultramafic soil at the Goro Plateau, New Caledonia



Fig. 2: *Araucaria columnaris* on a sandy coastal ground, Baie des Tortues, New Caledonia



Fig. 3: An *Araucaria laubenfelsii* seedling at Mont Do, New Caledonia

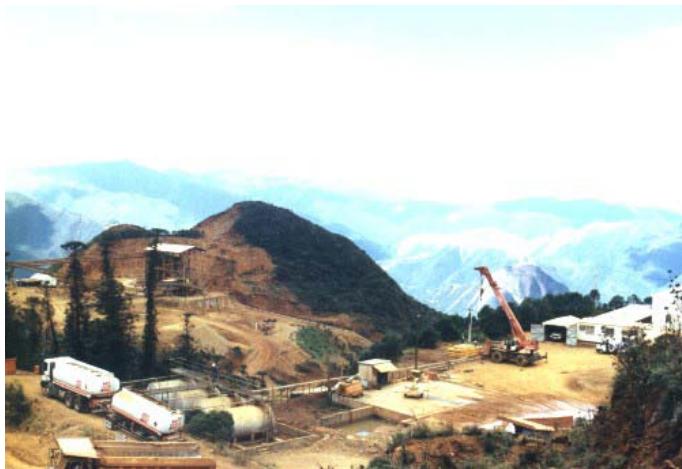


Fig. 4: Small remnants of *Araucaria montana* in a destroyed environment as a consequence of intensive Nickel mining at Mont Kaala, New Caledonia



Fig. 5: A fresh branchlet of *Araucaria Montana*



Fig. 6: *Araucaria rulei* on ultramafic soil at Col de Poro, New Caledonia

## Results

### Caledonian *Araucaria* beetles

Our field study in New Caledonia resulted in a sample of beetles comprising 33 species associated with *Araucaria columnaris*, *A. laubenfelsii*, *A. montana*, *A. muelleri* or *A. rulei* (Tab. 1, Annex). Only seven of these species could be determined of which just two (Anthribidae: *Aranthribus araucariae*; Curculionidae: *Dobionus arauacarinus*) had been recorded before from New Caledonian *Araucaria* trees. Three species of bark beetles (Curculionidae: Scolytinae) were new and have been described in the meantime as *Pachycotes grandis*, *P. engelsi* and *Xylechinus araucariae* (Mecke 2004a). The beetles of

the remaining 24 taxa could only be identified to genus or even higher levels. According to Kuschel (personal communication), who is studying the Cossoninae, Curculioninae and Dryophthorinae, this rest evidently contains 14 yet unidentified morphospecies, probably most of which will have to be described as new species. Four additional species - 1 still unidentified chrysomelid beetle (Eumolpinae) and the 3 nemonychids *Notomacer araucariae*, *N. hirtulus* and *N. caledonicus* - were recorded from other authors so that the currently known number of New Caledonian Araucaria beetles is 37.

### Synopsis of *Araucaria*-associated beetles

The result of the field studies and the bibliographic search is a list comprising a total of 233 beetle species using *Araucaria* trees as hosts (Tab. 1, Annex). These beetles belong to 17 families: Alleculidae, Anthribidae, Belidae, Biphyllidae, Brentidae, Buprestidae, Cerambycidae, Chrysomelidae, Cucujidae, Curculionidae (including the subfamilies Brachycerinae, Cossoninae, Curculioninae, Dryophthorinae, Platypodinae, Rhynchophorinae and Scolytinae), Lucanidae, Megalopodidae, Melandryidae, Nemonychidae, Nitidulidae, Oedemeridae and Silvanidae. According to the present taxonomic status, the araucariophagous beetles comprise 114 described genera and some taxa not fitting in any of these, thus presumably species for which a new genus has to be established.

Within the many beetles living on *Araucaria* trees, the most diverse family is Curculionidae with 148 species, followed by Cerambycidae (Figs. 7 – 8) with 32 and Nemonychidae with 24 taxa. Accordingly a great multiplicity of niches is occupied, and a remarkable richness of life histories evolved.



Fig. 7: Larva of the long-horned beetle *Taurorucus chabriacii* (Cerambycidae) in a branch of *Araucaria angustifolia*, Brazil



Fig. 8: The long-horned beetle of *Tithonus virescens* (Cerambycidae) from *Araucaria angustifolia*, Brazil

## Discussion

### ***Araucaria* beetles of presumed Gondwana origin**

Insect taxa with presumed Gondwana origin are considered those with an extant distribution on *Araucaria* trees in both biogeographic regions, the Neotropics and Oceania. On species or genus level there is no example of a taxon shared in both regions except for the worldwide distributed and extremely polyphagous bark beetle species *Hypothenemus eruditus* and *Xyleborus affinis* or the worldwide distributed genera *Syllitus* (Cerambycidae), *Platypus* (Fig. 9) (Curculionidae: Platypodinae), *Xylechinus* and *Xyleborus* (Curculionidae: Scolytinae).



Fig. 9: A male pin-hole borer of *Platypus araucariae* (Curculionidae, Platypodinae) from *Araucaria angustifolia*, Brazil

But there are tribes and subfamilies exclusively occurring on trees of the family Araucariaceae in South America and Oceania. One example is the subfamily Palophaginae (Megalopodidae), comprising 3 Australian beetle species whose larvae feed on pollen inside of male cones of *Araucaria* and *Agathis* (Kuschel & May 1990). Recently, the fourth member of this subfamily was discovered by Kuschel & May (1996) in the Neotropical Region in male cones of the Chilean *Araucaria araucana*.

Another example is the nemonychid tribe Mecomacerini, proposed by Kuschel (1994) for the four South American genera *Brarus* Kuschel (Fig. 10), *Mecomacer* Kuschel,

*Rhynchitomacerinus* Kuschel, *Rhynchitoplesius* Voss and the four Oceanian genera *Aragomacer* Kuschel, *Bunyaeus* Kuschel, *Eutactobius* Kuschel and *Notomacer* Kuschel (Tab. 1, Annex). All adults and larvae feed on pollen of Araucariaceae and, except for *Aragomacer leai* recorded from *Araucaria cunninghamii*, *Agathis atropurpurea* and *A. robusta* (Araucariaceae), the remaining 20 species are exclusively known from *Araucaria* trees in these two disjunct geographic regions.



Fig. 10: *Brarus mystes* (Nemonychidae) on a male cone of *Araucaria angustifolia*, Brazil

The Araucariini, a weevil tribe (Curculionidae, Cossoninae) erected by Kuschel (1966), is covering the neotropical genus *Araucarius* Kuschel and the four oceanian genera *Coptocorynus* Marshall, *Mastersinella* Lea, *Xenocnema* Wollaston and *Inosomus* Broun (Zarazaga & Lyal, 1999). The single species of the latter genus, *Inosomus rufopiceus* Broun 1881, is known from *Podocarpus* in New Zealand. These trees belong to the family Podocarpaceae which is adelphic to Araucariaceae and shows a similar disjunct distribution. The remaining 4 genera are exclusively associated with Araucariaceae: *Araucarius* with both South American *Araucaria* species, *Coptocorynus* with the Australian *Araucaria cunninghamii* and *Mastersinella* and *Xenocnema* with oceanian *Agathis* species (Kuschel, 1966).

All the beetle groups, found exclusively on Araucariaceae in both biogeographic regions, belong to the more archaic taxa within their respective families and share several primitive characters (Kuschel 1966, 1994, 1995, Kuschel & May 1990, Sequeira & Farrell 2001, Sequeira et al. 2000). In addition to their disjunct distribution, this confirms the assumption that the associations with *Araucaria* trees originate from Gondwanan periods. The extremely consistent microhabitat conditions under the bark or inside the male cones evidently conserved a very old and highly specialized araucariofauna.

### **Post-Gondwana associations of insects with *Araucaria* trees**

With exception of the taxa treated in the previous paragraph, most of the remaining taxa listed in Tab. 1 (Annex) have to be regarded post-Gondwanian newcomers on *Araucaria* trees. Their actual biogeographic distribution is either neotropical or oceanic. Of course this exclusive western or eastern occurrence could also result from former extinction of taxa in one of the regions of todays *Araucaria* populations.

### **Patterns of abundance and established feeding guilds of *Araucaria* beetles**

The relatively thick phloem of *Araucaria* trees is colonized by a distinct curculionid fauna composed of several *Araucaria* specialized genera of Cossoninae and Tomicini (Scolytinae) (Figs. 11 - 13). Male cones host an unique Nemonychidae (Fig. 10) and Palophaginae (Megalopodidae) fauna. According to *Araucaria* fossils, the reproductive

organs and the phloem did not change their morphological structure since cretaceous times (Stockey 1994) and, therefore, these plant organs preserved absolutely stable microclimatic conditions over extremely long periods. This seems to be the main reason for the high degree of specialization and the large number of primitive faunistic elements representing this portion of the araucariofauna (Kuschel 1966, 1994, 1995, Kuschel & May 1990). Within the entire disjunct distribution area of the extant *Araucaria* species, these four subfamilies comprise highly abundant taxa and a remarkable diversity within the araucariophagous insects. The beetles of nearly all of these 79 species are monophagous on *Araucaria* male cones and phloem, respectively, representing well established old feeding guilds on their host trees.



Fig. 11: The weevil *Araucarius kuscheli* (Curculionidae, Cossoninae) feeding on the phloem of *Araucaria angustifolia*, Brazil



Fig. 12: Galleries of the bark beetle *Xylechinus araucariae* (Curculionidae, Scolytinae) in the wood of *Araucaria laubenfelsii*, New Caledonia



Fig. 13: The bark beetle *Xylechinosomus contractus* (Curculionidae, Scolytinae), Brazil

### Microhabitat adaptations of the *Araucaria* entomofauna

Weevils of the tribe Araucariini (Curculionidae, Cossoninae) form the unique representatives of cossonine weevils that live and feed as adults inside of bark. As a special adaption to this microhabitat their large spinelike tibial hairs may be interpreted. Most bark beetles *sensu strictu* (Curculionidae, Scolytinae) also have such tibial structures, looking rather similar. This was considered by Kuschel (1966) to indicate a close phylogenetic relationship between Scolytionae and Cossoninae. As recently shown by SEM analyses, all these tibial structures are much enlarged true hairs rooted in a socket (Mecke, in press). They clearly facilitate the locomotion of bark tunneling beetles within their galleries (Fig. 14). Weevils of the tribe Araucariini (Fig. 11) are the only extant curculionids (Cossoninae, Curculioninae) that live as larvae and adults inside of the phloem like most bark beetles do and, therefore, like in the Scolytinae, their ancestral character of possessing giant tibial hairs has been preserved until today.



Fig. 14: Galleries of the weevil cf. *Dobionus* sp. (Curculionidae, Cossoninae) in a dead branch of *Araucaria montana*

### Co-speciation of beetles living exclusively on one or a few *Araucaria* species

Co-speciation of beetle genera with an at least Gondwanian *Araucaria* association took place in the neotropical genera *Araucarius* (Curculionidae, Cossoninae), *Sinophloeus*, *Xylechinosomus* (Fig. 13) (Curculionidae, Scolytinae) and *Mecomacer* (Nemonychidae, Rhinorhynchinae). *Sinophloeus* and *Mecomacer* are restricted to the Chilean *Araucaria araucana*. Beetles of the genera *Araucarius* and *Xylechinosomus* live on both South American *Araucaria* trees, but there is no species occurring on both *A. araucana* and *A. angustifolia* the geographic areas of which are separated from each other nowadays by more than 1,000 km and the Andean barriere.

In Oceania, the genera *Prospheres* (Buprestidae, Polycestinae), *Pachycotes*, *Hylurdreconus* (Curculionidae, Scolytinae), *Aragomacer* and *Notomacer* (Nemonychidae, Rhinorhynchinae) are restricted to *Araucaria* trees. Some of the beetle species belonging to these genera accept two or more *Araucaria* species as hosts, but except for *Hylurdreconus corticinus*, found on trees of all the three naturally occurring *Araucaria* species of Australia and Papua New Guinea, the remaining taxa are limited to *Araucaria* trees of one locality only.

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## Annex

Tab. 1: Taxonomic list of Coleoptera feeding on *Araucaria* trees. Abbreviations: **Host**: an = *A. angustifolia*, ar = *A. araucana*, br = *A. bihamata*, bi = *A. bidwillii*, cu = *A. cunninghamii*, co = *A. columnaris*, la = *A. laubenfelsii*, he = *A. heterophylla*, hu = *A. hunsteinii*, mo = *A. montana*, mu = *A. muelleri*, ru = *A. rulei*, sp. = species not identified. **Origin**: AR = Argentinien, AU = Australia, BR = Brazil, CH = Chile, NC = New Caledonia, NI = Norfolk Island, NZ = New Zealand, PN = Papua New Guinea.

**Observations:** br = in branches, ne = needles, se = in seeds (female cones), st = in strobili (male cones), tr = in trunks. **References:** 1 = McKeown (1938); 2 = Marshall (1948); 3 = Zajciw (1962); 4 = Schedl (1964); 5 = Viana (1965); 6 = Kuschel (1966); 7 = Schedl, (1966a); 8 = Schedl (1966b); 9 = Vernalha (1967); 10 = Gray (1968); 11 = Silva et al. (1968); 12 = Marinoni (1969); 13 = Voss (1971); 14 = Schedl (1972); 15 = Gray (1974); 16 = Schedl, 1976; 17 = Levey (1978a); 18 = Levey (1978b); 19 = Peredo et al. (1980); 20 = Hoffmann (1981); 21 = Schönherr & Pedrosa-Macedo (1981); 22 = Browne (1984); 23 = Pedrosa-Macedo & Schönherr (1985); 24 = Wood (1985); 25 = Galileo (1987); 26 = Costa et al. (1988); 27 = Hawkswood (1990); 28 = Wood & Bright (1992); 29 = Barriga et al., (1993); 30 = Lyal (1993); 31 = Kuschel (1994); 32 = Schönherr (1994); 33 = Barreto et al. (1996); 34 = Kuschel & May (1996); 35 = Morrone (1997); 36 = Bright & Skidmore (1997); 37 = Kuschel & May (1997); 38 = Kuschel (1998); 39 = Klein Koch & Waterhouse (2000); 40 = Kuschel (2000); 41 = Mecke (2000); 42 = Mecke et al. (2000); 43 = Kuschel et al. (2000); 44 = Mecke et al. (2001); 45 = Mecke (2002); 46 = Mecke (2004a); 47 = Mecke (2004b); 48 = Mecke & Galileo (2004); 49 = Beaver (pers. com.); 50 = Jolivet (pers. com.); 51 = Lawson (pers. com.); 52 = Mecke (pers. obs.); 53 = Schneider (pers. com.). Unpublished species records are printed in **bold letters**

Taxa	Host	Origin	Observ.	References
<b>Alleculidae</b> – Alleculinae				
<i>Lobopoda dallieri</i> Pic, 1927	an	BR	br	44,45
<b>Anthribidae</b> – Anthribinae				
<i>Aranthribus araucariae</i> Kuschel, 1998	br,la	NC	br	38, <b>52</b>
<i>Cacephatus</i> sp.	he	NI		38
Choraginae				
<b><i>Araecerus bicristatus</i> Blackburn, 1900</b>	cu	AU		<b>51</b>
<b>Belidae</b> – Oxyonychinae				
<i>Oxycraspedus cornutus</i> Kuschel, 1959	ar	CH	se	35,40
<i>Oxycraspedus cribricollis</i> (Blanchard, 1851)	ar	CH	se	35,40
<i>Oxycraspedus minutus</i> (Philippi & Philippi, 1864)	ar	CH	se	35,40
<b>Biphyllidae</b>				
<i>Diplocoelus</i> cf. <i>amplicollis</i> Reitter, 1877	an	BR	st	26

<b>Brentidae – Taphroderinae</b>				
<i>Taphroderes sahlbergi</i> (Sharp, 1895)	an	BR	br	44,45
<b>Buprestidae – Buprestinae</b>				
<i>Araucariana queenslandica</i> Levey, 1978	cu	AU		17
<b>Chalcophorinae</b>				
<i>Baudonisia villosiventris</i> (Chevrolat, 1938)	an	BR	tr	3,11,44,45
<i>Euchroma gigantea</i> Linnaeus, 1758	an	BR	tr	11,45
<b>Polycestinae</b>				
<i>Prospheres alternecostata</i> Levey, 1978	cu,hu.	PN	tr, br	18
<i>Prospheres aurantiopicta</i> (Laporte & Gory, 1838)	cu	AU	tr	18
<b>Prospheres chrysocomus</b> Fauvel, 1891	co	NC	tr	<b>52</b>
<i>Prospheres norfolkensis</i> Levey, 1978	he	NI		18
<b>Cerambycidae – Cerambycinae</b>				
<b>Diotimana undulata</b> (Pascoe, 1859)	cu	PN		<b>51,53</b>
<i>Epipodocarpus andinus</i> Bosq, 1951	ar	CH	br	19,29
<i>Grammicosum flavofasciatum</i> Blanchard, 1843	ar	CH	tr,br	19
<i>Huequenia araucana</i> (Cerda, 1980)	ar	CH		29
<i>Huequenia livida</i> (Germain, 1898)	ar	CH		29
<i>Paraholopterus nahuelbutensis</i> Cerda & Cekalovic, 1986	ar	CH		29
<b>Strongylurus decoratus</b> (McKeown, 1940)	cu	AU		<b>51</b>
<i>Syllitus araucariae</i> McKeown, 1938	cu	AU		1
<i>Syllitus schajovskoi</i> Bosq, 1953	ar	CH		19
<b>Lamiinae</b>				
<b>Acanthocinini (4 spp., indet.)</b>	la	NC		<b>52</b>
<i>Acanthoderes juno</i> Fisher, 1938	an	BR	tr	3,11,20
<i>Acalolepta tincturata</i> Pascoe, 1866	cu	PN		27
<b>Dysthaeta anomala</b> Pascoe, 1859	cu	AU		<b>51</b>
<b>Enicodes fichteli</b> (Schreibers, 1802)	la	NC		<b>52</b>
<i>Estola hirsutella</i> Aurivillius, 1922	ar	CH	br	19,29
<i>Leptostylus perniciosus</i> Monné & Hoffmann, 1981	an	BR		20
<i>Potemnemus detzneri</i> Kriesche, 1923	cu,hu	PN		53
<i>Steirastoma marmoratum</i> Thunberg, 1822	an	BR		12,20,45
<i>Taurorus chabriacii</i> Thomson, 1857	an	BR	br,se	11,12,20,44,45
<i>Taurorus mourei</i> Marinoni, 1969	an?	BR		12,44,45
<i>Tithonus virescens</i> (Melzer, 1931)	an	BR		44,45
<i>Urgleptes</i> sp.	an	BR		20
<b>Lepturinae</b>				
<b>Strangalia dimidiata</b> (Redtenbacher, 1867)	an	BR	br	44,45
<b>Parandrinae</b>				
<i>Hesperandra glabra</i> (De Geer, 1774)	an	BR	tr	3,11,20,44
<i>Parandra araucana</i> Bosq, 1951	ar	CH	tr	19,29
<b>Prioninae</b>				
<i>Microplophorus calverti</i> Philippi, 1897	ar	CH	tr	19
<i>Microplophorus penai</i> Galileo, 1987	ar	CH		25,29
<b>Olethrius tyrannus</b> Thomson, 1860	co	NC	tr	<b>52</b>
<b>Chrysomelidae – Chrysomelinae</b>				
<i>Calligrapha polypila</i> Germar, 1821	an	BR	ne	9,45
<b>Eumolpinae</b>				
<b>Gen. sp. indet.</b>	an	BR	ne	<b>52</b>
<b>Gen. sp. indet.</b>	sp.	NC		<b>50</b>
<b>Cucujidae</b>				
<i>Laemophloeus minutus</i> Olivier, 1791	an	BR	se	11
<b>Curculionidae – Brachycerinae</b>				
<b>Aesiotes notabilis</b> Pascoe, 1865	cu	AU		<b>51</b>
<i>Oribius destructor</i> (Marshall, 1957)	cu	PN	br	10
<b>Cossoninae</b>				
<i>Araucarius brasiliensis</i> Kuschel, 1966	an	BR	br	6,41,45,48
<i>Araucarius chilensis</i> Kuschel, 1966	ar	CH	br	6,35,40
<i>Araucarius crassipunctatus</i> Mecke, 2000	an	BR	br	6,41,48

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<i>Araucarius kuscheli</i> Mecke, 2000	an	BR	br	6,41,45,48
<i>Araucarius major</i> Kuschel, 1966	ar	CH	tr	6,35,40
<i>Araucarius medius</i> Kuschel, 1966	ar	CH	tr	6,35,40
<i>Araucarius minor</i> Kuschel, 1966	ar	CH	br	6,35,40
<i>Araucarius ruehmi</i> Kuschel, 1966	an	BR	br,tr,st	6,35,40
<i>Coptocorynus araucariae</i> Marshall, 1948	cu	AU		2,6
<i>Dobionus araucarinus</i> Kuschel, 2000	br,la,ru	NC	tr, br	43,52
<b><i>Dobionus brachyrhinus</i> (Montrouzier, 1861)</b>	co	NC	br	52
<b><i>Dobionus</i> sp.</b>	co	NC	br	52
<b>cf. <i>Dobionus</i> spp. (6 species)</b>	co,la,mo,mu,ru	NC	br	52
<i>Eurycorynophorus scabriculus</i> Voss, 1964	an	BR	br	42,44,45,48
<i>Micromimus</i> sp.	an	BR	br	44,48
<b>cf. <i>Ochrananus</i> sp.</b>	mo	NC	br	52
<i>Pseudostenoscelis araucariae</i> Voss, 1971	cu	PN	tr	13
<b><i>Rhyncolus longicollis</i> (Montrouzier, 1861)</b>	co	NC	tr	52
Curculioninae				
<i>Achopera araucariae</i> Marshall, 1948	cu	AU		2
<i>Araucarietius viridans</i> Kuschel, 1952	ar	CH	st	35,40
<i>Calvertius tuberosus</i> (Fairmaire & Germain, 1860)	ar	CH	tr	35,40
<i>Eisingius araucariae</i> Kuschel, 2000	ar	CH	st	35,40
<i>Eisingius chusqueae</i> (Bondar, 1949)	ar	CH	st	35,40
<b><i>Eurhamphus fasciculatus</i> Schuckard, 1838</b>	cu	AU		51
<i>Heilipodus tuberculatus</i> (Boheman, 1836)	an	BR	tr	42,44,45,48
<b><i>Ilacuris laticollis</i> Pascoe, 1865</b>	cu,hu	AU,PN		51,53
<i>Mallus costatus</i> Marshall, 1948	cu	AU		2
<b><i>Mechistocerus</i> sp.</b>	co	NC	br	52
<b><i>Mitrasethus australiae</i></b>	cu,hu	AU,PN		51,53
<i>Mitrasethus baridioides</i> Redtenbacher, 1868	he	NZ	tr	30
<b><i>Orthorhinus cylindrirostris</i> (Fabricius)</b>	cu	AU		51
<b><i>Orthorhinus patruelis</i> (Fabricius)</b>	cu	PN		53
<i>Planus barbatus</i> Kuschel, 1952	ar	CH	se	40
<b><i>Scelodolichus</i> sp.</b>	mu	NC	tr	52
<i>Spermologus rufus</i> Boheman, 1843	an	BR	se	33,48
<b><i>Tyrtaeosus microthorax</i> Pascoe, 1870</b>	cu	AU		51
<i>Vanapa oberthuri</i> Pouillaude, 1915	cu	PN		10
Dryophthorinae				
<b><i>Dryophthorus</i> spp. (4 species)</b>	mo,mu	NC	br,tr	52
Platypodinae				
<i>Cenocephalus thoracicus</i> Chapuis, 1865	an	BR		7,48
<b><i>Crossotarsus barbatus</i> Chapuis, 1865</b>	hu	PN	tr	49
<i>Diapus nanus</i> Schedl, 1969	cu,hu	PN	tr	28,49
<i>Diapus papuans</i> Schedl, 1968	hu	PN		28
<b><i>Diapus pusillimus</i> Chapuis, 1865</b>	hu	PN		49
<i>Diapus quinquespinatus</i> Chapuis, 1865	hu	PN		28
<b><i>Dinoplatypus pseudocupulatus</i> (Schedl, 1935)</b>	cu	PN		49
<i>Euplatypus parallelus</i> (Fabricius, 1801)	cu	AU		28
<i>Platypus araucariae</i> Schedl, 1966	an	BR	tr	7,21,45,48
<i>Platypus froggatti</i> Sampson, 1926	cu	AU		28
<b><i>Platypus geminatus</i> Chapuis, 1865</b>	hu	PN		49
<i>Platypus jansoni</i> Chapuis, 1865	cu,hu	AU,PN		28
<i>Platypus mutatus</i> Chapuis, 1865	an	BR	tr	16,21,48
<i>Platypus omnivorus</i> (Lea, 1904)	cu	AU		7
<i>Platypus opacideclivis</i> Schedl, 1969	cu	PN		28
<i>Platypus parallelus</i> (Fabricius, 1801)	an	BR	tr,se	16,48
<i>Platypus praepositus</i> Schedl, 1969	hu	PN		28
<i>Platypus queenslandi</i> Schedl, 1936	cu	AU		28
<i>Platypus semigranosus</i> (Sampson, 1925)	cu	AU		7
<i>Platypus subgranosus</i> Schedl, 1936	cu	AU		7
<i>Platypus varipennis</i> Schedl, 1968	cu	PN		28
<i>Tesserocerus insignis</i> Saunders, 1936	an	BR		7,21,45,48
<b><i>Treptoplatypus australis</i> (Chapuis, 1865)</b>	cu	AU		7
Rhynchophorinae				
<i>Sitophilus oryzae</i> Linnaeus, 1763	an	BR	se	11,48
Scolytinae, BOTHROSTERNINI				

<i>Cnesinus dividuus</i> Schedl, 1938	an	BR		23,48
<i>Pagiocerus punctatus</i> Eggers, 1928	an	BR	st	16,23,48
<b>CORTHYLINI</b>				
<i>Araptus araucariae</i> (Schedl, 1966)	an	AR	se	8,48
<i>Corthylus papulans</i> Eichhoff, 1868	an	BR	br	44,48
<i>Corthylus praecultus</i> Schedl, 1976	an	BR	br	42,44,45,48
<i>Corthylus rufopilosus</i> Eggers, 1931	an	BR	br	42,44,48
<i>Monarthrum brasiliensis</i> (Schedl, 1936)	an	BR	se	21,23,48
<i>Pityophthorus anticus</i> Schedl, 1976	an	BR	br,se,st	16,21,45,48
<b>CRYPHALINI</b>				
<i>Cryphalus araucariae</i> Schedl, 1969	cu	PN		28
<i>Cryphalus brunneus</i> Browne, 1984	hu	PN		22
<i>Cryphalus cylindrus</i> Browne, 1984	hu	PN		22
<i>Cryphalus diversicolor</i> Browne, 1984	hu	PN		22
<b><i>Cryphalus</i> spp. (5 species)</b>	co,la,mu	NC		52
<b><i>Cryphalus tetricus</i> (Schedl, 1940)</b>	cu,hu	PN		49
<i>Cryptocarenus seriatus</i> Eggers, 1933	an	BR	br	21,23,48
<i>Hypothenemus eruditus</i> Westwood, 1836	an,cu,co,hu,	BR,PN,NC	br	15,48,52
<b>PHLOEOSININI</b>				
<i>Hyleops glabratus</i> Schedl, 1938	cu	AU		7
<b>PHLOEOTRIBINI</b>				
<i>Phloeotribus argentinensis</i> (Schedl, 1951)	an	AR,BR	se	5,48
<i>Phloeotribus cylindricus</i> Schedl, 1951	an	BR	br	5,48
<b>TOMICINI</b>				
<i>Chaetoptelius impar</i> Schedl, 1975	hu	PN		28
<i>Hylurdretonus araucariae</i> Schedl, 1964	cu	PN	br	4,7,10
<i>Hylurdretonus corticinus</i> Wood, 1980	bi,cu,he,hu	AU,PN		28,49
<i>Hylurdretonus nanus</i> Browne, 1984	cu	PN		22
<i>Hylurdretonus piniarius</i> Schedl, 1938	bi,cu,	AU		7
<i>Hylurgonotus armaticeps</i> Schedl, 1955	ar	CH	tr	35,40
<i>Hylurgonotus tuberculatus</i> (Eggers, 1942)	ar	CH	tr	35,40
<i>Pachycotes araucariae</i> Schedl, 1975	cu	PN		28
<i>Pachycotes australis</i> Schedl, 1938	cu	AU		28
<i>Pachycotes clavatus</i> Schedl, 1938	cu	AU		28
<i>Pachycotes engelsi</i> Mecke, 2004	mu	NC	tr	46
<i>Pachycotes grandis</i> Mecke, 2004	la,mu	NC	tr	46
<i>Pachycotes kuscheli</i> Schedl, 1972	he	NI		14
<i>Pachycotes minor</i> Wood, 1985	cu	AU		28
<i>Pachycotes peregrinus</i> (Chapuis, 1869)	sp.	NZ		28
<i>Sinophloeus antipodus</i> (Eggers, 1942)	ar	CH	br	35,40
<i>Sinophloeus porteri</i> (Brèthes, 1922)	ar	CH		35,40
<i>Sinophloeus solidus</i> (Schedl, 1976)	ar	CH	br	35,40
<i>Xylechinosomus brasiliensis</i> (Schedl, 1951)	an	BR	br	16,21,23,48
<i>Xylechinosomus contractus</i> (Chapuis, 1873)	an	BR	br,tr,se	5,7,16,45,48
<i>Xylechinosomus hirsutus</i> Schedl, 1963	an	BR	br,se	7,21,23,48
<i>Xylechinosomus humilis</i> (Blanchard, 1851)	ar	CH		36
<i>Xylechinosomus lucianae</i> Mecke, 2004	an	BR	br	47,48
<i>Xylechinosomus minimus</i> Schedl, 1963	an	BR	br,tr,se,st	7,21,23,45,48
<i>Xylechinosomus paranaensis</i> (Schönher, 1994)	an	BR	br,tr	32,48
<i>Xylechinosomus pilosus</i> Wood, 1985	an	BR		24,48
<i>Xylechinosomus bicolor</i> (Philippi & Philippi, 1864)	ar	CH		35,40
<i>Xylechinus araucariae</i> Mecke, 2004	la	NC	br	46
<i>Xylechinus porteri</i> (Brèthes, 1925)	ar	CH		28
<b>XYLEBORINI</b>				
<i>Ambrosiodmus catharinensis</i> (Eggers, 1928)	an	BR	br	44,48
<i>Ambrosiodmus compressus</i> (Lea, 1893)	bi,cu	AU		7,28
<i>Arixyleborus canaliculatus</i> (Eggers, 1923)	cu	PN		15
<i>Coptodryas eucaalyptica</i> (Schedl, 1938)	cu	AU		7,28
<i>Coptodryas intermedius</i> (Eggers, 1923)	cu	PN		15
<i>Coptodryas libra</i> (Eggers, 1923)	cu	PN		15
<i>Cryptoxyleborus gracilior</i> Browne, 1984	cu	PN		22,28
<i>Eccoptopterus spinosus</i> (Olivier, 1795)	cu	PN		15
<i>Euwallacea barbatus</i> (Hagedorn, 1910)	cu	AU,PN		15,28

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<i>Euwallacea piceus</i> Motschulsky, 1863	cu	PN		15
<i>Euwallacea wallacei</i> (Blandford, 1896)	cu	PN		49
<i>Xyleborinus linearicollis</i> (Schedl, 1937)	an	BR	br	16,21,23,48
<i>Xyleborinus sentosus</i> (Eichhoff, 1868)	an	BR		7,21,23,45,48
<i>Xyleborus adelographus</i> Eichhoff, 1868	an	BR	se	16,21,23,48
<i>Xyleborus affinis</i> Eichhoff, 1868	an,cu	BR,AU		16,21,23,45,48
<i>Xyleborus andrewesi</i> (Blandford, 1896)	cu	PN		15
<i>Xyleborus ferrugineus</i> (Fabricius, 1801)	an	BR	br,se	7,21,23,48
<i>Xyleborus gratiosus</i> Schedl, 1975	cu	PN		28
<i>Xyleborus nitellus</i> Browne, 1984	cu	PN		22
<i>Xyleborus perforans</i> (Wollaston, 1857)	cu,hu,	AU,PN		7,15
<i>Xyleborus perplexus</i> Schedl, 1969	cu	PN		28
<i>Xyleborus similis</i> ; Ferrari, 1867	cu	AU		28
<i>Xyleborus volvulus</i> (Fabricius, 1775)	an	BR		16,21,23,48
<b><i>Xylosandrus morigerus</i> (Blandford, 1894)</b>	<b>cu</b>	<b>PN</b>		<b>49</b>
<i>Xylosandrus pseudosolidus</i> Schedl, 1936	cu	AU		28
<b>Lucanidae</b>				
<i>Sclerognathus fairmairei</i> Parry	ar	CH		39
<b>Megalopodidae – Palophaginae</b>				
<i>Palophagoides vargasorum</i> Kuschel, 1996	ar	CH	st	34
<i>Palophagus australiensis</i> Kuschel, 1990	cu	AU		34
<i>Palophagus bunyae</i> Kuschel, 1990	bi	AU	se	34
<b>Melandryidae</b>				
<i>Eudircea laticornis</i> Champion, 1916	an	BR	br	44
<i>Megapsilaphus sexnotatus</i> (Champion, 1916)	an	BR	br	44
<b>Nemonychidae – Rhinorhynchinae</b>				
<i>Aragomacer grayi</i> Kuschel, 1994	cu	PN		31
<i>Aragomacer leai</i> Kuschel, 1994	cu	AU		31
<i>Aragomacer munus</i> Kuschel, 1994	hu	PN		31
<i>Aragomacer papuae</i> Kuschel, 1994	cu	PN		31
<i>Aragomacer uniformis</i> Kuschel, 1994	cu	AU		31
<i>Basiliogeus prasinus</i> Kuschel, 1994	bi	AU		31
<i>Basiliogeus striatopunctatus</i> (Lea, 1926)	cu	AU		31
<i>Basiliorhinus araucariae</i> Kuschel, 1994	bi	AU		31
<i>Brarus mystes</i> Kuschel, 1997	an	BR	st	37,44
<i>Bunyaeus eutactae</i> Kuschel, 1994	cu	AU		31
<i>Bunyaeus monteithi</i> Kuschel, 1994	bi	AU		31
<i>Eutactobius puellus</i> Kuschel, 1994	cu	AU		31
<i>Mecomacer collaris</i> (Voss, 1952)	ar	CH	st	35,40
<i>Mecomacer hirticeps</i> Kuschel, 1954	ar	CH	st	35,40
<i>Mecomacer ruficornis</i> Kuschel, 1955	ar	CH	st	35,40
<i>Mecomacer scambus</i> Kuschel, 1954	ar	CH	st	35,40
<i>Notomacer araucariae</i> Kuschel, 1994	br	NC		31
<i>Notomacer eximius</i> Kuschel, 1994	cu	AU		31
<i>Notomacer hirtulus</i> Kuschel, 1994	br	NC		31
<i>Notomacer reginae</i> Kuschel, 1994	cu	AU		31
<i>Notomacer zimmermani</i> Kuschel, 1994	cu	AU		31
<i>Notomacer caledonicus</i> Kuschel, 1994	co	NC		31
<i>Rhynchitomacerinus kuscheli</i> (Voss, 1952)	ar	CH	st	35,40
<i>Rhynchitoplesius eximius</i> (Voss, 1937);	an	BR	st	26,37
<b>Nitidulidae</b>				
<i>Conotelus</i> sp.	an	BR		26
<b>Oedemeridae</b>				
<i>Copidita</i> sp.	an	BR		44
<b>Silvanidae</b>				
<i>Ahasverus</i> sp.	an	BR		44

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