Australian Journal of Entomology (2004) **43**, 114–128

Jumping across Wallace's line: *Allodessus* Guignot and *Limbodessus* Guignot revisited (Coleoptera: Dytiscidae, Bidessini) based on molecular-phylogenetic and morphological data

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Abstract The monotypic genus *Allodessus* (Coleoptera: Dytiscidae: Bidessini) has previously been considered to be strictly Australian, with *A. bistrigatus* (Clark) having a wide range on that continent and in Tonga. Based on data gathered from extensive museum collections and a molecular phylogeny of the group, this concept is revised. The following species of the Bidessini are now assigned to *Allodessus*: *Bidessus megacephalus* Gschwendtner (East Palearctic), *Liodessus oliveri* Ordish (New Zealand), *Bidessus skottsbergi* Zimmermann (Chile: Easter Island) and *Bidessus thienemanni* Csiki (Indonesia: Java). The latter, as well as *L. oliveri*, are morphologically extremely similar to *A. bistrigatus* and are, perhaps, the same species. As currently delimited, *Allodessus* has a wide range, spanning parts of the Australian, Oriental, Palearctic and Oceanian regions. Based on a cladistic analysis of mtDNA sequence data, we synonymize *Boongurrus* Larson and *Tjirtudessus* Watts & Humphreys with *Limbodessus* Guignot. Australian species of *Liodessus* Guignot are transferred to *Limbodessus*, which is the sister group of *Allodessus*. The following 33 species are transferred to *Limbodessus*: Oceania – *Liodessus cheesmanae* (Balfour-Browne 1939) [Vanuatu], *Bidessus curviplicatus* Zimmermann 1927 [Samoa]; Australian epigean–*Bidessus dispar* Sharp 1882, *B. praelargus* Lea 1899, *Hydroporus amabilis* Clark 1862, *H. gemellus* Clark 1862, *B. inornatus* Sharp 1882, *B. Shuckardii* Clark 1862; Australian hyporheic – *Boongurrus rivulus* Larson 1994; Australian stygobiont – *Nirridessus bigbellensis* Watts & Humphreys 2000, *N. challaensis* Watts & Humphreys 2001, *N. cueensis* Watts & Humphreys 2000, *N. fridaywellensis* Watts & Humphreys 2001, *N. hinkleri* Watts & Humphreys 2000, *N. lapostaae* Watts & Humphreys 1999, *N. masonensis* Watts & Humphreys 2001, *N. morgani* Watts & Humphreys 2000, *N. pinnaclesensis* Watts & Humphreys 2001, *N. pulpa* Watts & Humphreys 1999, *N. windarraensis* Watts & Humphreys 1999, *Tjirtudessus bialveus* Watts & Humphreys 2003, *T. cunyuensis* Watts & Humphreys 2003, *T. eberhardi* Watts & Humphreys 1999, *T. hahni* Watts & Humphreys 2000, *T. jundeeensis* Watts & Humphreys 2003, *T. karalundiensis* Watts & Humphreys 2003, *T. macrotarsus* Watts & Humphreys 2003, *T. magnificus* Watts & Humphreys 2000, *T. raesidensis* Watts & Humphreys 2001, *T. silus* Watts & Humphreys 2003, *T. sweetwatersensis* Watts & Humphreys 2003, *T. wilunaensis* Watts & Humphreys 2003, *T. yuinmeryensis* Watts & Humphreys 2003. *Limbodessus compactus* (Clark) has a wide Asian/Australian range, while all other *Limbodessus* spp. are endemic to the Australian region and represent an adaptive radiation of epigean, hyporheic and subterranean species, as well as numerous undescribed New Guinea high-altitude specialists. Another species of Bidessini, *Papuadessus pakdjoko* Balke, is newly recorded from Papua New Guinea here.

Key words *Allodessus*, *Limbodessus*, cladistics, biogeography, mtDNA, Australia, Bidessini

INTRODUCTION

The more than 500 world species of Bidessini (Hydroporinae) are mainly smaller than 5 mm and represent most of the smaller species of diving beetle or Dytiscidae. Bidessines inhabit a wide range of aquatic habitats, such as stream margins, peat bogs, high-altitude pools and all kinds of wetland pools and ditches rich in vegetation. With the exception of the groundwater species, Bidessini rather prefer more insulated habitats than fully shaded deep-forest sites. Many species are strong dispersers and can be attracted by light traps in huge numbers. In Australia there are 11 genera of Bidessini (after Watts 2002) and more than 60 species, most of them occurring in underground waters (Watts & Humphreys 1999, 2000, 2001, 2003; many new species unpublished).

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The monotypic genus *Allodessus* Guignot (Coleoptera: Dytiscidae, Hydroporinae) has previously been considered an Australian endemic, with *A. bistrigatus* (Clark) as its unique species (Watts 1978, 1985, 2002; Biström 1988; Nilsson 2001) (see Table 1 for authors and dates of species). Larson (1993) mentioned an undescribed species from Queensland, for which there are no further data, that is likely to be identical with a new species of *Liodessus* Guignot currently under description by Watts and Leys (pers. comm. 2002). According to the molecular phylogenetic hypothesis for the relationships of the Australian Bidessini published by Cooper *et al*. (2002), *Allodessus* is either the sister group of a clade comprising the Australian *Liodessus*, *Limbodessus* Guignot, *Boongurrus* Larson and *Tjirtudessus* Watts & Humphreys (including *Nirridessus*, cf., Watts & Humphreys 2003), or subordinated within this clade.

During a partial revision of New Guinea Bidessini, one of us (MB) had the opportunity to study many species from the Oriental and Australian regions. *Liodessus oliveri* Ordish (New Zealand: Kermadec Islands) and *Bidessus thienemanni* Csiki (Indonesia: Java) were found to be extremely similar to *A. bistrigatus* (Clark), if not the same species. Similarly, *Bidessus megacephalus* Gschwendtner (East China, Japan), and *Bidessus skottsbergi* Zimmermann (Chile: Easter Island) share with *Allodessus* a well-defined morphology of the male parameres (=lateral lobes of penis), leading to the impression that all these species should be considered within the same genus. This would then have an Australian, Oceanian, Oriental and Palearctic range.

Cooper *et al*. (2002) presented a molecular phylogenetic hypothesis for the relationships of the Australian Bidessini, focusing on the groundwater fauna. Using their data, complemented with newly obtained sequences (including the recently described *Papuadessus pakdjoko* Balke 2001), we test the monophyly of a potentially extended *Allodessus* and its phylogenetic position with respect to the clade comprising the Australian *Liodessus*, *Limbodessus*, *Boongurrus* and *Tjirtudessus* (Balke 2000; Cooper *et al*. 2002). We also provide new diagnoses of *Allodessus bistrigatus*, *A. megacephalus, A. oliveri*, *A. skottsbergi* and *A. thienemanni,* as well as additional illustrations and collecting localities for *Papuadessus pakdjoko*. Finally, we re-examine the classification of the Australian *Liodessus*, *Limbodessus*, *Boongurrus* and *Tjirtudessus* lineage in the light of our findings and those of Cooper *et al*. (2002), as well as morphological evidence (Balke unpubl. data 2000).

MATERIALS AND METHODS

Morphology

Beetles were studied using a Leitz MZ12 dissecting microscope at 10–100×. Illustrations were made with the help of a drawing tube. Inked drawings were scanned and mounted using the CorelDRAW® 8.0 package, which was also the tool for assembling the map.

Table 1 List of species included in the analyses, with authorities and dates of description

HYDROPORINAE
Bidessini
Allodessus bistrigatus (Clark 1862)
Allodessus oliveri (Ordish 1966)
Allodessus megacephalus (Gschwendtner 1931)
Bidessodes bilita Watts (1978)
Bidessodes mjobergi (Zimmermann 1924)
Clypeodytes migrator (Sharp 1882)
Gibbidessus chipi Watts (1978)
Hydroglyphus balkei Hendrich 1999
Hydroglyphus daemeli (Sharp 1882)
Limbodessus amabilis (Clark 1862)
Limbodessus challaensis (Watts & Humphreys 2001)
Limbodessus compactus (Clark 1862)
Limbodessus cueensis (Watts & Humphreys 2000)
Limbodessus dispar (Sharp 1882)
Limbodessus eberhardi (Watts & Humphreys 1999)
Limbodessus fridaywellensis (Watts & Humphreys 2001)
Limbodessus hinkleri (Watts & Humphreys 2000)
Limbodessus inornatus (Sharp 1882)
Limbodessus magnificus (Watts & Humphreys 2000)
Limbodessus masonensis (Watts & Humphreys 2001)
Limbodessus praelargus (Lea 1899)
Limbodessus pulpa (Watts & Humphreys 1999)
Limbodessus raesidensis (Watts & Humphreys 2001)
Limbodessus rivulus (Larson 1994)
Limbodessus shuckardii (Clark 1862)
Papuadessus pakdjoko Balke (2001)
Uvarus picipes (Lea 1899)
Hydroporini
Necterosoma dispar (Germar 1848)
Nirripirti hinzae Watts & Humphreys (2001)
Carabhydrini
Carabhydrus niger Watts (1978)
COPELATINAE
Copelatus haemorrhoidalis (F. 1787) (Germany: Bavaria, vii.2001, Balke & Kotrba)
COLYMBETINAE
Colymbetes paykulli Erichson 1837 (Germany: Brandenburg, viii.2002, Hendrich)
DYTISCINAE
Dytiscus circumcinctus Ahrens 1811 (Germany: Brandenburg, viii.2002, Hendrich)

The beetles mentioned in this paper are housed in the following institutions and private collections: BMNH, The Natural History Museum (former British Museum of Natural History), London, UK; cGW, Prof Dr G. Wewalka collection, Vienna, Austria; BPBM, Bernice P. Bishop Museum, Honolulu, Hawaii, USA; cLH, Lars Hendrich collection, Berlin, Germany; cMB, Michael Balke collection, Berlin, Germany; MNZT, Museum of New Zealand Te Papa Tongarewa (formerly Dominion Museum), Wellington, New Zealand; NMW, Naturhistorisches Museum Wien, Austria; OLML, Oberösterreichisches Landesmusem, Linz, Austria; ZSM, Zoologische Staatssammlung München, Germany. Abbreviations in the taxonomic treatment of the species are: orig. descr., original description; descr., work containing descriptive notes; cat., species mentioned in systematic catalogues; ecol., notes on ecology; faun., notes on distribution.

Taxon sampling

In addition to the species sampled in Cooper *et al*. (2002), we obtained sequences of *Bidessus megacephalus*, *Liodessus oliveri*, an additional specimen of *Allodessus bistrigatus* from Adelaide, and *Papuadessus pakdjoko*. Outgoups were three species of Hydroporinae non-Bidessini (also obtained from Cooper *et al*. 2002) plus three non-Hydroporinae (*Dytiscus circumflexus* Ahrens 1811, *Colymbetes paykulli* Erichson 1837 and *Copelatus haemorrhoidalis* (F. 1787)). All the Australian Bidessini genera are thus represented, with the exception of *Kintingka* Watts & Humphreys (a sytgobiont genus for which no specimens were available (Cooper *et al*. 2002), and which might not be a Bidessini). Collection data for the newly sequenced specimens are in the material sections of the respective species, and in Table 1 for the non-hydroporine outgroup species.

DNA extraction and sequencing

Specimens for DNA extraction were collected in 96% ethanol and processed following either the procedures outlined in Cooper *et al.* (2002) or in Ribera *et al*. (2001). Two contiguous fragments of mitochondrial DNA were sequenced, one containing part of the 3′ end of the cytochrome oxidase I gene (COI), and another containing the 3′ end of the large ribosomal subunit (16S rRNA), plus the complete tRNALeu and about 100 basepairs of the 5′ end of the NADH dehydrogenase subunit 1 (ND1) (see Cooper *et al*. 2002 for primers). New sequences have been submitted to GenBank (Accession numbers: AY368222-AY368230).

Phylogenetic analyses

COI and ND1 sequences were not length variable, and 16S rRNA and tRNALeu sequences were aligned in Clustal W using the default options (Thompson *et al*. 1994), and modified by hand to correct obvious mismatches. Due to length variability, some regions could not be unambiguously aligned, and were deleted in some of the analysis (see below). The final aligned matrix is available at http://www.waterbeetles.info/allodessus.htm.

Phylogenetic analyses of aligned sequence data were conducted in the program PAUP* 4.0b10 (Swofford 2002). Parsimony analyses were performed using TBR heuristic searches of 2000 random addition sequences, coding gaps as a missing character. Node support was assessed with non-parametric bootstrapping (Felsenstein 1985), with 1000 pseudoreplicates and 50 random additions per pseudoreplicate. Partitioned Bremer support values (Baker & DeSalle 1997) were computed using TreeRot (Sorenson 1996) in combination with PAUP. We assessed significance of the Incongruence Length Difference (ILD) (Farris *et al*. 1994) with the Partition Homogeneity Test (PHT) as implemented in PAUP, using a heuristic search of 1000 replicates with 50 random addition sequences each.

RESULTS

Phylogenetic analyses and morphological interpretation

The analysis of the combined COI, 16S rRNA, trRNALeu and ND1 sequences using all characters resulted in three equally parsimonious trees (Table 2), in the strict consensus of which the two sampled specimens of *Allodessus bistrigatus* form a monophyletic group together with *Bidessus megacephalus* and *Liodessus oliveri*. This lineage (‘*Allodessus* lineage’ from now on) is placed in a polytomy with the species of *Boongurrus*, *Tjirtudessus*, *Limbodessus*, and the Australian *Liodessus* (‘*Limbodessus* lineage’ from now on). After reweighting the characters *a posteriori* according to the rescaled consistency index, a single most parsimonious tree was found, in which the *Allodessus* and *Limbodessus* lineages are, respectively, monophyletic and sisters (Fig. 1). Sister to this clade of the above genera is a group comprising *Bidessodes*, *Gibbidessus* and *Uvarus*, and sister to all the genera *Clypeodytes*, *Papuadessus* and the species of *Hydroglyphus* [note: we here only refer to Australian *Bidessodes* and *Uvarus* which may be generically different from their American type species].

When the characters containing gaps were removed (57 nucleotide positions, Table 2), the search (all characters

Table 2 Tree statistics, length, and support for key nodes in the different analyses

Dataset	No. aligned characters	No. informative characters	No. equally parsimonious trees	Length (no. steps) of the most parsimonious tree	Consistency index (CI)	*Allodessus* lineage	*Limbodessus* lineage	*Allodessus* plus *Limbodessus* clade
Combined, all characters	1435	467	3	2478	0.38	+	?	+
Reweighted			1		0.69	+	+	+
Gaps excluded	1378	445	1	2390	0.37	+	+	+
COI	611	233	75	1395	0.34	+	?	?
Reweighted			1		0.61	+	–	+
16S all characters	824	234	88	1053	0.44	?	+	+
Reweighted			3		0.72	+	+	+
16S gaps excluded	767	212	4	967	0.43	?	+	+
Reweighted			3		0.73	+	+	+

+, node present; ?, node unresolved; –, node not present.

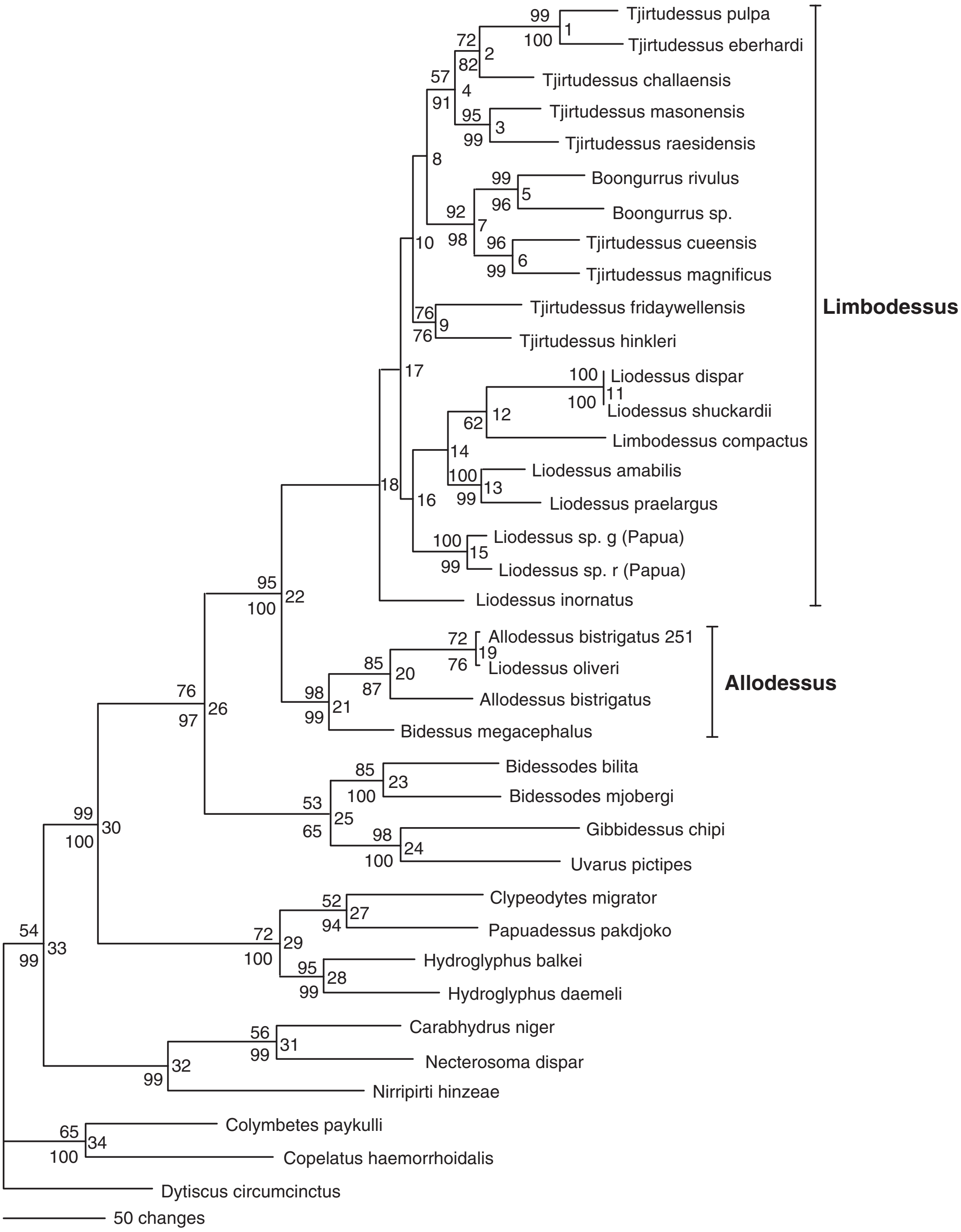

Fig. 1. Phylogram of the single most parsimony tree obtained after removing characters that include gaps (see Text and Table 2). The topology of the tree is identical to that obtained with the reweighed characters when all characters were included. Numbers indicate non-parametric bootstrap support (only values above 50%). Above branches, all characters, reweighed; below branches, gaps excluded, equal weight. Numbers inside nodes refer to Table 3.

equally weighted) resulted in a single most parsimonious tree, with an identical topology to the reweighted tree using all characters (Fig. 1). In both cases, the *Allodessus* lineage has strong support (bootstrap of 98 and 99%, respectively), as well as the node including the *Allodessus* plus *Limbodessus* lineages (bootstrap of 95 and 100%, respectively, Fig. 1). The *Limbodessus* lineage, although recovered in both the (reweighted) tree using all characters and that excluding the gaps, is only weakly supported (less than 50% bootstrap, combined Bremer support of 1 or 0, respectively, Fig. 1, Table 3).

The Partition Homogeneity Test indicated significant incongruence among the two mitochondrial contiguous fragments (COI and 16Sr RNA + tRNALeu + ND1, $P = 0.01$, both excluding gaps and with all characters). The partitioned Bremer support values (PBS) reflected this incongruence, with an abundance of negative support in both partitions (COI and

16S, Table 3). The correlations of the PBS values with the combined Bremer support indicate that when all characters were used, the main signal was provided by the COI partition, while in the analysis with the gaps excluded, the main signal was that of the 16S partition. The correlations between the PBS and global Bremer values were, however, positive and highly significant in all cases (Table 4). In general, the lack of significant negative correlations suggests that the signal is either congruent or independent, but there is no significant contradiction (Table 4).

Searches were conducted on the separate fragments to further explore the origin of the incongruence, and how it could affect the taxonomic conclusions of our analyses. The search on the COI sequence resulted in 75 equally parsimonious trees, the strict consensus of which was largely unresolved, with a basal polytomy including all genera of Bidessini in the analysis (not shown). The *Allodessus* lineage was, however, still recovered as monophyletic, in agreement with the combined analyses. After reweighting according to the rescaled consistency index, a single most parsimonious tree was found, with a topology largely consistent with that of the combined analyses. The main difference was the placement of two species of *Liodessus* (*L. dispar* and *L. shuckardii*), which were sister to the *Allodessus* lineage, and not included in the *Limbodessus* lineage, as in the combined analyses.

Table 3 Partitioned Bremer Support values for the nodes of the optimal trees obtained using all characters and excluding characters with gaps

Node	All characters			Gaps excluded		
	COI	16S	Combined	COI	16S	Combined
1	6.7	4.3	11	5	7	12
2	–2.6	5.6	3	–3.6	7.6	4
3	1.2	6.8	8	–0.7	8.7	8
4	–3.3	4.3	1	–3.6	6.6	3
5	13.7	–2.7	11	9	3	12
6	1.2	5.8	7	–0.5	8.5	8
7	2.9	5.1	8	0.4	6.6	7
8	–2.3	2.3	0	–1.9	3.9	2
9	3.2	1.8	5	–3	7	4
10	–1.8	1.8	0	–2	3	1
11	27.7	10.3	38	14.3	24.7	39
12	0.7	0.3	1	–4.6	7.6	3
13	14.7	–4.7	10	11	–1	10
14	–1.8	1.8	0	–3.5	4.5	1
15	9.7	–0.7	9	9.1	0.9	10
16	–1.8	1.8	0	–1.1	2.1	1
17	–1.8	1.8	0	–1.1	2.1	1
18	–1.8	1.8	0	–3.5	4.5	1
19	0	1	1	–0.6	1.6	1
20	5.7	–3.7	2	2	0	2
21	8.2	–2.2	6	4.3	1.7	6
22	11.7	2.3	14	0	11	11
23	1.7	4.3	6	–1.3	9.3	8
24	10.7	3.3	14	7	6	13
25	–1.8	1.8	0	–5	6	1
26	–2.8	6.8	4	–6	12	6
27	4.7	–2.7	2	1	1	2
28	4.7	3.3	8	1	7	8
29	3.7	2.3	6	0	5	5
30	3.2	15.8	19	1	16	17
31	3.2	–0.2	3	3	2	5
32	3.2	–0.2	3	2	2	4
33	3.2	–0.2	3	3	2	5
34	5.2	1.8	7	2.5	3.5	6

Node, number of the node (see Fig. 1); COI, cytochrome oxidase I partition; 16S, 16S rRNA + trRNALeu + ND1 partition; combined, combined (global) Bremer support.

The analysis of the 16Sr RNA + tRNALeu + ND1 fragment including all characters resulted in a strict consensus tree in which the *Limbodessus* lineage was recovered as monophyletic, and sister to a polytomy including the species within the *Allodessus* lineage, which was not fully resolved. After reweighting the characters according to the rescaled consistency index, three most parsimonious trees were found (Table 2) in which the *Allodessus* and *Limbodessus* lineages were each monophyletic and sisters, in agreement with the combined analyses. The analyses excluding characters with gaps gave identical results, both for the equal weight and the reweighted trees.

The monophyly of the *Allodessus* lineage (*Allodessus bistrigatus*, *Bidessus megacephalus* and *Liodessus oliveri*) is thus strongly supported in most of the analyses (Table 2). A potential synapomorphy of this lineage is the claw shape of the parameres (Fig. 4d, see below). In other Bidessini genera, the apical segment of the parameres is either long and fingerlike, or otherwise modified (Biström 1988; Balke 2000). Although we could not obtain specimens of *Bidessus thienemanni* and *Bidessus skottsbergi* suitable for genetic studies, they have the same paramere structure as the species of the *Allodessus* lineage (in addition to a similar general morphology), so we hypothesise their placement in the lineage and consider all of them as part of an extended genus *Allodessus*. The presence of modified antennal segments 8–10 in the female, with diagonal basal grooves (Fig. 4a–c), is an apomorphy for all *Allodessus* species except for *A. skottsbergi*, where the female antennomeres all lack such a groove, which is the plesiomorphic state. Also, in the clade *A. bistrigatus* + *A. megacephalus* + *A. oliveri* + *A. thienemanni*, there is sexual dimorphism of the abdominal colouration, which is yellow in females, but mainly blackish in the males. In *A. skottsbergi*, the abdomen is yellow in both sexes (this dimorphism is absent in related genera). *Allodessus skottsbergi* would thus be sister to the *Allodessus* species. According to our results, *L. oliveri* is sub-

Table 4 Correlations between Partitioned Bremer Support values and the global Bremer support for the analyses with all characters and excluding characters with gaps (only significant values at $P < 0.05$)

	allCOI	all16S	allcom.	gCOI	g16S
all16S	n.s.				
allcom.	0.85	0.50			
gCOI	0.90	n.s.	0.70		
g16S	0.33	0.84	0.74	n.s.	
gcom.	0.83	0.50	0.99	0.70	0.75

all, analysis with all characters; g, analysis excluding characters with gaps; COI, Cytochrome Oxidase I partition; 16S, 16S rRNA + trRNALeu + ND1 partition; com., combined (global) Bremer support.

ordinated within *A. bistrigatus* (both specimens from South Australia). Both species are similar morphologically, but with the present information it is not possible to determine its taxonomic status with more detail, especially as the sequence data for our two specimens of *A. bistrigatus* are rather incomplete with one full 16S sequence missing.

Although the support for the monophyly of the *Limbodessus* lineage is not as strong as that for *Allodessus* (Table 2, see also Cooper *et al*. 2002), it is either present or unresolved in all the analyses, with the only exception being the reweighted tree of the COI sequence in isolation. Within the *Limbodessus* lineage none of the included genera form a monophyletic lineage in any of the trees with the exception of the two species of *Boongurrus* sampled. In our opinion the best option is thus to consider the whole *Limbodessus* lineage as a single genus, which for priority reasons should be named *Limbodessus*.

SYSTEMATICS

Genus *Allodessus* Guignot

Allodessus Guignot 1953: 110.

Type species. *Hydroporus bistrigatus* Clark 1862, by original designation (Guignot 1953: 110; see also Nilsson *et al*. 1989; Nilsson 2001).

Diagnosis. ***Length.*** 2.1–3.5 mm. ***Habitus.*** Body elongate, more or less dorsoventrally depressed (Figs 2a–c, 3a–e). ***Structural features.*** With cervical line on head (Figs 5a,b); with pronotal and elytral plica (elytral plica may be absent or short in some individuals of *A. skottsbergi*) (Figs 5a,b); no sutural line on elytron; elytral epipleuron without basal cavity and carina (Fig. 5c).

Remarks. The character identifying the genus *Allodessus* is the shape of the parameres, with the second segment being claw-shaped (Fig. 4d). Otherwise species of *Allodessus* much resemble those of *Limbodessus* (see also Biström 1988; under *Liodessus*): body rather elongate; median lobe of aedeagus more or less simply curved with no conspicuous modifications; epipleuron without basal cavity which would be delimited by a carina (only present in *Limbodessus compactus* (Clark), see below); head usually with a 'line' between hind angles of eyes; pronotum and elytron usually with basal plica.

Checklist of and key to *Allodessus* species

A. bistrigatus (Clark) – Australia, Tonga.
A. megacephalus (Gschwendtner), **n. comb.** – E China, Taiwan, Japan.
A. oliveri (Ordish), **n. comb.** – New Zealand.
A. skottsbergi (Zimmermann), **n. comb.** – Easter Island (Chile).
A. thienemanni (Csiki), **n. comb.** – Java (Indonesia).

1 Smaller species, 2.1–2.5 mm long, venter yellow in both sexes, dorsum yellowish, elytral plica short or absent (Fig. 3e), Easter Island .... *A. skottsbergi*
Larger species, 2.7–3.5 mm long, abdomen yellow in females and mainly black in males, dorsum yellowish and usually with obscure darker pattern on elytron, elytral plica long and always present (Figs 2a–c and 3a-d) 2

2 Four very similar species, that are best identified based on their distribution: *A. megacephalus* (Japan and China), *A. bistrigatus* (Australia, Tonga), *A. oliveri* (New Zealand), *A. thienemanni* (Indonesia: Java). The two latter are likely synonyms of *A. bistrigatus*.

Allodessus bistrigatus (Clark) (Figs 2a–c,3a–c, 3f–h,4d,5,6)

Hydroporus bistrigatus Clark 1862: 419 (orig. descr.).
Bidessus bistrigatus (Clark): Watts 1963: 28 (descr.).
Allodessus bistrigatus (Clark): Guignot 1953: 110 (descr.); Watts 1978: 44 (descr.), 1985: 24 (faun.); Timms & Watts 1987: 3 (ecol.); Biström 1988: 19 (descr.); Larson 1993: 49 (ecol.); Bayly 1997: 169 (ecol.); Nilsson 2001: 109 (see this cat. for synonyms).

Type locality. Australia: Moreton Bay.

Types. Lectotype male: 'Lectotype', 'Type', '67.56', 'bistrigatus/Clark/australia', 'Hydroporus bistrigatus clk, Det. C. Watts 1974' (BMNH).

Other material examined. ***Australia.*** We studied more than 100 specimens from all over Australia (BMNH; cLH; NMW); we newly sequenced: 1 individual, South Australia, Adelaide, Scott's Creek Conservation Park, xii.2001, Balke & Watts (NHM, DNA voucher Michael Balke 251). ***Tonga.*** 2 males, 'Type', 'Tonga, Nr. Nukualofa, Olo Olo, large permanent pond, 26.x.1953', 'Brit. Mus. 1987–14', 'aL5', 'Bidessus tongaensis Type!, J. Balfour-Browne det. xi.1953', 'Liodessus J. Balfour-Browne det. 1967' [unpublished name] (BMNH); 4, Tonga, Tapu, Nuku alofa, 5.ii.1985, Starmühlner (cGW).

Diagnosis. ***Length.*** 2.7–3.3 mm (Australia), 2.8–3.3 mm (Tonga, cGW). ***Habitus.*** Elongate, with slight discontinuity in lateral outline between pronotum and elytron; pronotum appears widest slightly in front of middle, its lateral sides appear subparallel over basal half (Figs 2a,3a,c). **Male.** ***Colour.*** Body and appendages yellowish to ferrugineous. Head ferrugineous, posterior to cervical line darker, brownish. Pronotum bright ferrugineous. Elytron ferrugineous with obscure (Fig. 3a–c) to well defined (Figs 2a,b) darker patch on posterior half, sometimes larger patch or larger patch broken into 2 patches, however, entire elytron sometimes rather unicolour yellowish, or dark patch may extend towards pronotum and almost reach it with fingerlike extension; sometimes with darker sutural angle (Figs 2a,b,3a–c). Metasternum, metacoxal plate and metacoxal process blackish; epipleuron yellow; ventrite 1 yellowish, 2–5 blackish with yellowish lateral margins, last ventrite blackish laterally, medially yellowish. Ventrites sexually dimorphic (see below). ***Surface sculpture.*** Head moderately densely punctate on frons; punctation on clypeus and posteriorly sparse; impunctate posterior to cervical line. Head with microreticulation on frons (Fig. 5b); clypeus shiny; with fine microreticulation posterior to cervical line (Fig. 5b). Pronotum with moderately dense punctation; sparser laterally and close to plica. Size of punctures as on head. Pronotum

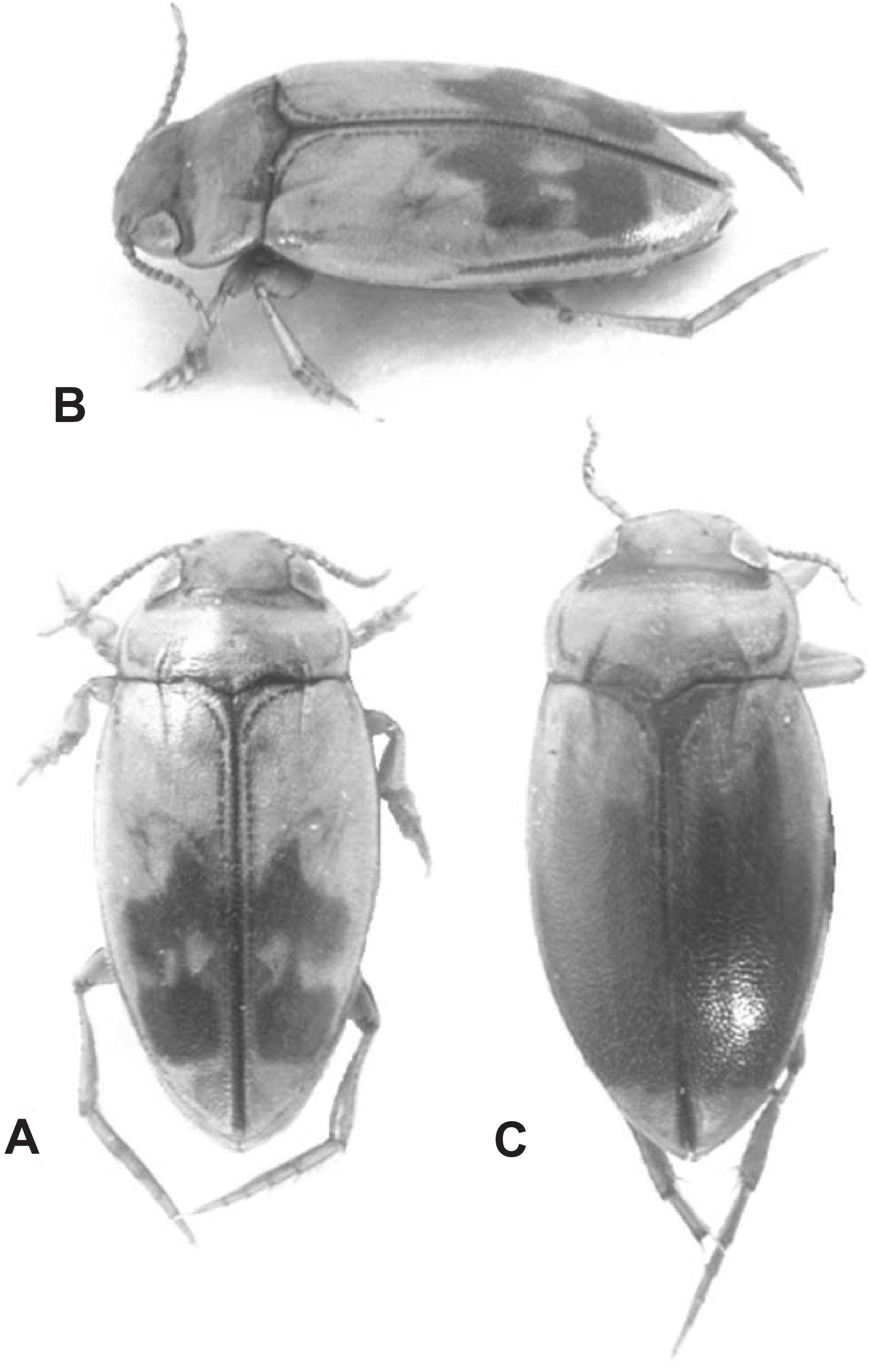

Fig. 2. *Allodessus bistrigatus*, habitus: (a,b) Western Australia; (c), Tonga, Nukualofa. The Australian specimen is comparably freshly eclosed and brightly coloured. The dark elytral pattern is usually not that sharply delimited.

without microreticulation. Elytron with moderately dense and evenly distributed punctation; without microreticulation. Metasternum almost impunctate, venter including epipleuron with some larger punctures; shiny, without microreticulation (Figs 5c,fd). ***Structural features.*** Cervical line present and comparatively distinct (Figs 5a,b); no sutural line present. Pronotal and eltyral plicae present and long; pronotal plica somewhat to distinctly sinuate. Pronotum with distinct bead laterally. Epipleuron without basal cavity. Metacoxal lines diverging anteriorly; not reaching metasternal wings (Fig. 5d). Ventrite 6 with distinct bead forming a rim, a few short and stout setae visible there; continuously rounded, apically with acute tip. Antenna long, stout (Fig. 3f). ***Genitalia.*** Median lobe comparatively strongly curved (Fig. 3h). Paramere as in Figure 4d. **Female.** Abdomen yellowish. Antennomere 8 slightly, 9 and 10 strongly modified, narrowed at base due to

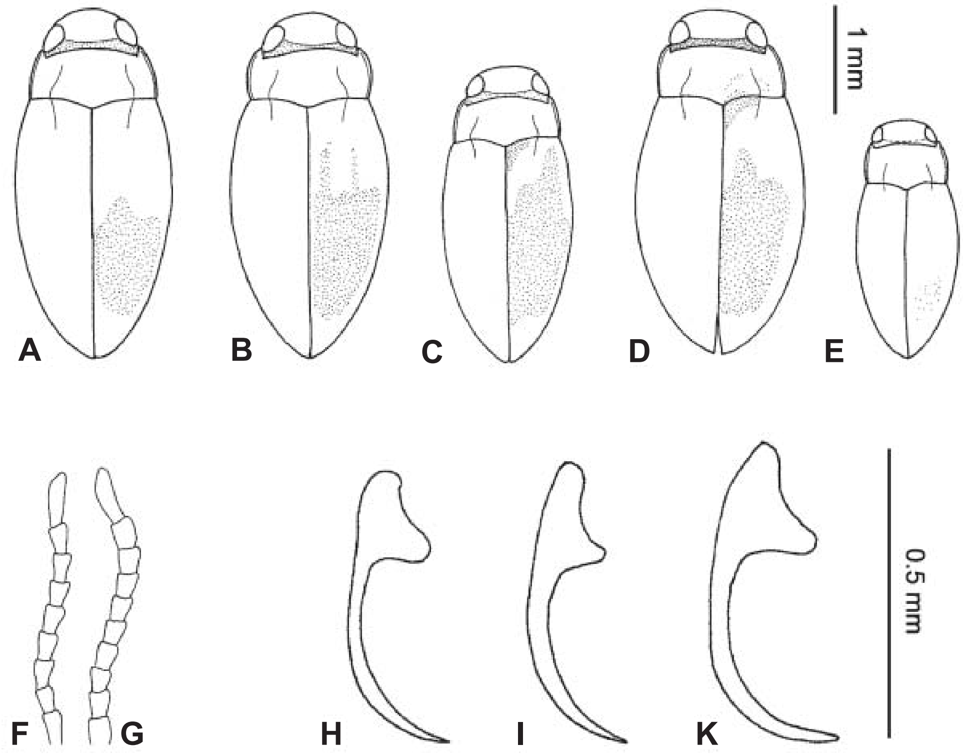

Fig. 3. *Allodessus* spp. (a–e) habitus: (a) *A. bistrigatus*, Australia; (b) *A. bistrigatus*, Tonga, Nukualofa; (c) *A. bistrigatus*, Tonga, Tapu, small specimen; (d) *A. megacephalus*, Japan; (e) *A. skottsbergi*; (f–g) *A. bistrigatus*, antenna (not to scale): (f) male; (g) female; (h–k) median lobe of aedeagus in lateral view: (h) *A. bistrigatus*, Australia; (i) *A. oliveri;* (k); *A. megacephalus*, Japan.

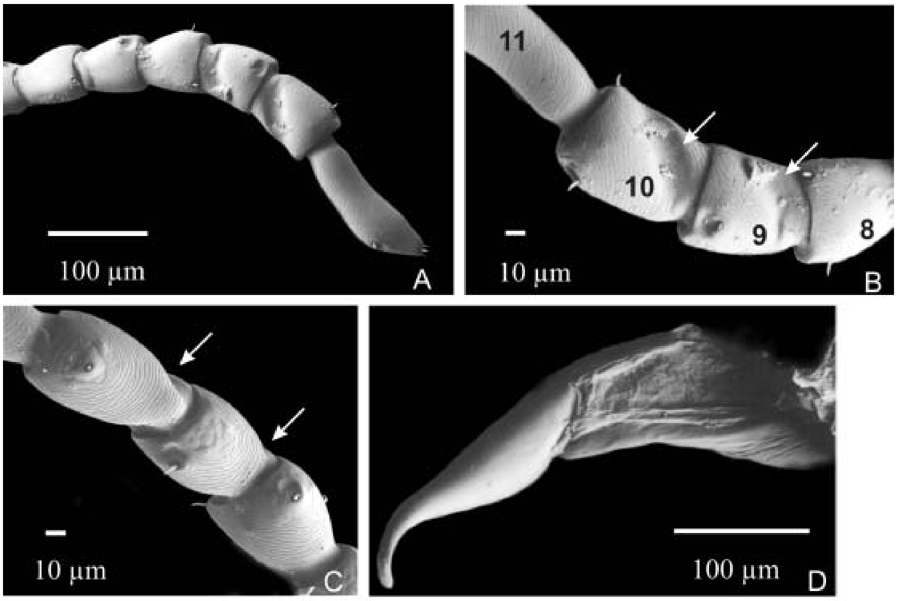

Fig. 4. *Allodessus* spp. (a–c) antenna of female of *A. megacephalus*, Japan: (a) dorsal view; (b) antennomeres 8–11, dorsal view, arrows point to grooves; (c) lateral view, antennomeres 7–11, arrows point to grooves on antennomeres 9 and 10; (d) paramere, *A. bistrigatus*, Australia.

presence of diagonal depressions, or grooves, on dorsal and ventral surface (as in Fig. 4a–c); antenna appearing long but slightly stouter than in male (Fig. 3g).

Remarks. The two Tonga specimens from BMNH differ from other *A. bistrigatus* by the more cordiform pronotum (Figs 2c,3b), and were labelled as '*Bidessus tongaensis'* by J. Balfour-Browne. This is an unpublished name. At first inspection we believed that these specimens could represent a different species, but four individuals from Tonga borrowed from cGW perfectly agree with Australian examples. The high variability of Tonga specimens deserves further attention as new material become available.

Larson (1993) lists an '*Allodessus*, new species' from Queensland. This species appears still to be under study. We have not seen specimens.

Distribution. Australia and Tonga (Fig. 6).

Habitat. *Allodessus bistrigatus* is common in temporary and permanent dams/ponds and other still waters in arid inland Australia. These water bodies are often muddy, seldom with much vegetation. In wetter areas, the species occurs in similar

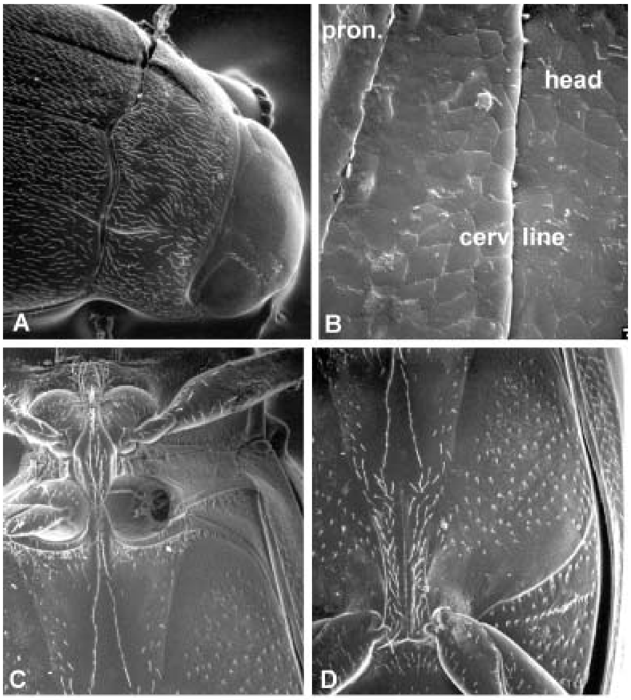

Fig. 5. *Allodessus bistrigatus*, male: (a) head, pronotum and base of elytron in a dorsolateral view; (b) head and anterior margin of pronotum (pron.): showing cervical line (cerv. line) and microreticulation on head; (c) ventral aspect of head, prosternum and metaventrite; (d) ventral aspect mainly showing metaventrite and metacoxae.

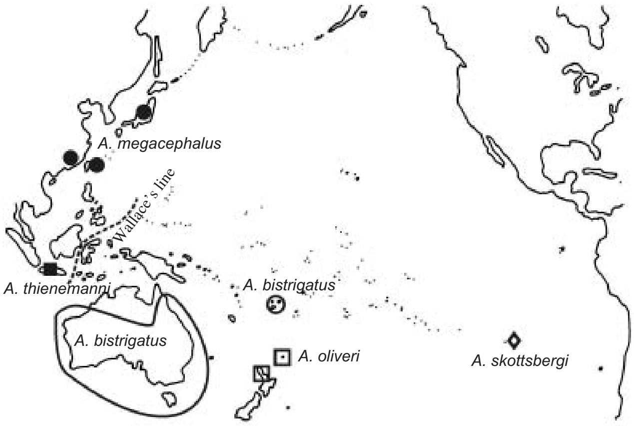

Fig. 6. Distribution of *Allodessus* spp.

habitats, as well as in slow-moving temporary streams where it is usually less abundant but still can be common. It is rare in the north and on the east coast. It is a strong flier, attracted to light and a mobile species that is well adapted to exploiting temporary water in arid areas (C. Watts, pers. comm. 2001). Larson (1993) reports the species from rice fields and other temporary ponds, which have at least partly a clay bottom. Bayly (1997) found the species in pools ('gnammas') on granite outcrops.

Allodessus megacephalus (Gschwendtner), n. comb. (Figs 3d,k,4a–c,6)

Bidessus megacephalus Gschwendtner 1931a: 21 (orig. descr.); Zaitsev 1953: 122 (descr.).

Bidessus maculosus Gschwendtner 1931b: 462 (orig. descr.); Zaitsev 1953: 122 (descr.).

Bidessus tokunagai Kamiya 1932: 5 (orig. descr.).

Liodessus megacephalus (Gschwendtner): Nilsson 1995: 51 (faun.); Nilsson 2001: 130 (cat.).

Type locality. ***Taiwan.*** Koto Sho Island. (*B. maculosus*: China: Fujian; *B. tokunagai*: Japan: Honshu: Seto).

Types. ***megacephalus.*** 1 male syntype, 'Koto Sho, 10 III-14 IV.1920, Coll. T.O. Kuni', 'Type Gschw.', 'Coll Gschwendtner', 'Bidessus megacephalus Gschw., det. Gschwendtner', 'Type', 'Allodessus megacephalus (Gsch), det. M. Balke 2001' (OLML). ***maculosus.*** 1 female syntype, 'Amoy', 'Type Gschw.', 'Dyt 51', 'Coll Gschwendtner', 'Bidessus maculosus Gschw., det. Gschwendtner', 'Type', 'Allodessus maculosus (Gsch), det. M. Balke 2001' (OLML). ***tokunagai.*** No types seen.

Other material examined. ***Hong Kong.*** 1 male, Tai Po Kau, downstream, 21–22.vi.1984, D. Dudgeon (NMW). Japan. 26, Cape Miura, Kanagawa, 3.i.1987, T. Abe & A. Sasai (cMB; NMW); we newly sequenced: 1 individual, Hamamatsu City, Nakatajima dune, 27.viii.2000, J. Bergsten (collection Ribera, DNA IR 608).

Diagnosis. ***Length.*** 3.1–3.5 mm. ***Habitus.*** Elongate, with slight discontinuity in lateral outline between pronotum and elytron; pronotum appears widest slightly in front of middle, its lateral sides appear subparallel over basal half (Fig. 3d). **Male.** ***Colour.*** Body and appendages yellowish to ferrugineous. Head ferrugineous, posterior to cervical line darker, brownish. Pronotum bright ferrugineous. Elytron ferrugineous with obscure to well-defined darker pattern posteriorly, pattern may have fingerlike extension towards pronotum and may sometimes almost reach pronotal base (Fig. 3d). Metasternum, metacoxal plate and metacoxal process blackish; epipleuron yellow; ventrite 1 yellowish, 2–5 blackish with yellowish lateral margins, last ventrite blackish laterally, medially yellowish. ***Surface sculpture.*** Head moderately densely punctate on frons; punctation on clypeus and posteriorly sparse; impunctate posterior to cervical line. Head with indistinct microreticulation on frons; clypeus shiny, with distinct microreticulation posterior to cervical line. Pronotum with moderately dense punctation; sparser laterally and close to plica. Size of punctures as on head. Pronotum without microreticulation. Elytron with moderately dense and evenly distributed punctation; without microreticulation. Metasternum almost impunctate, venter including epipleuron with some larger punctures; shiny, without microreticulation. ***Structural features.*** Cervical line present and comparatively distinct; no sutural line present. Pronotal and elytral plicae present and long; pronotal plica somewhat to distinctly sinuate. Pronotum with distinct bead laterally. Epipleuron without basal cavity. Metacoxal lines diverging anteriorly; not reaching metasternal wings. Ventrite

6 with distinct bead forming a rim, a few short and stout setae visible on hind margin of ventrite 6 in front of that rim; hind margin continuously rounded, apically with acute tip. Antenna long, stout (as in Fig. 3f). ***Genitalia.*** Median lobe as in Figure 3k. Paramere as in Figure 4d. **Female.** As in male, except as follows. Head and pronotum dull, finely chagreened, elytron also appearing somewhat dull; venter with ventrites 3–6 finely chagreened. Abdomen yellowish. Antennomere 8 slightly, 9 and 10 stronger modified, narrowed at base due to presence of diagonal depression on dorsal and ventral surface (Fig. 4a–c); antenna appearing long but slightly stouter than in male (as in Fig. 3g).

Remarks. According to Gschwendtner (1931a,b), there were four types of *B. megacephalus* and two of *B. maculosus*, from OLML, where his collection is deposited. We have so far been able to study only one example of each.

Distribution. Japan; Taiwan; E China (Fujian); S China (Nilsson 1995) (Fig. 6). Interestingly, Gschwendtner 1931b) and Zaitzev 1953) have reported this species (under the name *Bidessus megacephalus*) from Java.

Habitat. Ponds.

Allodessus oliveri (Ordish), n. comb. (Figs 3i,6)

Liodessus oliveri Ordish 1966: 230 (orig. descr.), 1967: 3 (descr.), 1976: 155 (descr.); Biström 1988: 19 (cat.); Nilsson 2001: 131 (cat.).

Type locality. New Zealand: Kermadec Islands.

Types. Holotype male (after Ordish), Kermadec Islands, viii.1908, W.R.B. Oliver (MNZT). There are 5 paratypes also from the Kermadec Islands, and 1 paratype from Sunday Island (Canterbury Museum, Christchurch, New Zealand) (MNZT).

Other material examined. ***New Zealand.*** 8, Kermadec Islands, Raoul Island, Denham Bay, 2 m, 19–21.x.1962, G.A. Samuelson (BPBM); we newly sequenced: 1 male, AK, Auckland City, Newmarket Park pond, 36°52′S 174°47′E, 1.vi.2002, S.E. Thorpe (BMNH) (DNA voucher Michael Balke 158).

Diagnosis. ***Length.*** 3.0–3.2 mm. ***Habitus.*** As in *A. bistrigatus*. See Fig. 1. This species is extremely similar to *A. bistrigatus* (see the description by Watts 1978; the description above). The only difference we could discerne is the slightly less curved median lobe in *A. oliveri* (Fig. 3i). We assume this species is a synonym of *A. bistrigatus*, but suggest studying sequence data from its type locality in relation to more sequence data from a wider range of Australian *A. bistrigatus* to resolve this problem.

Distribution. Kermadec Islands, New Zealand (Ordish 1966), Auckland (Fig. 6).

Habitat. Ponds.

Allodessus skottsbergi (Zimmermann), n. comb. (Figs 3e,6)

Bidessus skottsbergi Zimmermann 1924: 303 (orig. descr.).

Liodessus skottsbergi (Zimmermann): Biström 1988: 19 (cat.); Nilsson 2001: 131 (cat.).

Type locality. Chile: Easter Island: Rano Kao.

Types. 6 syntypes, ‘Osterinsel’, ‘Polynesien’, ‘Type (male)’, ‘Samml. A. Zimmermann’, and ‘Typus’ or ‘Paratypus’ (ZSM). The ‘Typus’ and ‘Paratypus’ labels were subsequently attached to the beetles by ZSM staff. Zimmermann did not designate a holotype.

Diagnosis. ***Length.*** 2.1–2.5 mm. ***Habitus.*** Elongate, with slight discontinuity in lateral outline between pronotum and elytron; pronotum appears widest slightly anterior to middle (Fig. 3e). **Male.** ***Colour.*** Body and appendages yellowish to ferrugineous. ***Surface sculpture.*** Head moderately densely punctate on frons; punctation on clypeus and posteriorly sparse; impunctate posterior to cervical line. Head without obvious microreticulation on frons; clypeus shiny; with fine microreticulation of longish meshes posterior to cervical line. Pronotum with moderately dense punctation; sparser laterally and close to plica. Size of punctures as on head. Pronotum without microreticulation. Elytron with moderately dense and evenly distributed punctation, punctures larger than on pronotum; without microreticulation. Metasternum almost impunctate, venter including epipleuron with some larger punctures; shiny, without microreticulation. ***Structural features.*** Cervical line present and comparatively distinct; no sutural line present. Pronotal plica present and long; elytral plica shorter and may be absent. Pronotal plica distinctly sinuate. Pronotum with distinct bead laterally. Epipleuron without basal cavity. Metacoxal lines parallel; not reaching metasternal wings. Ventrite 6 with distinct bead forming a rim, few short and stout setae visible there; continuously rounded, apically with acute tip. ***Genitalia.*** Median lobe slightly curved only (little less than in Fig. 3h). Paramere as in Figure 4d. Antenna long and stout. **Female.** Colour, including venter, as in male. Punctation as in male; entire body finely chagreened and thus appearing dull. Antennomeres 8–10 not modified. Antenna long and stout.

Distribution. Chile: Easter Island (Fig. 6).

Habitat. Crater lake, under algae (Zimmermann 1924).

Allodessus thienemanni (Csiki), n. comb. (Fig. 6)

Bidessus thienemanni Csiki 1938: 128 (orig. descr.); Brinck 1948: 5.

Hydroglyphus thienemanni (Csiki): Biström 1988: 14 (cat.); Nilsson 2001: 126 (cat.).

Bisessus megacephalus Gschwendtner: Gschwendtner 1931b: 462 (partim) (descr.); Zaitsev 1953: 122 (partim) (descr.).

Type locality. Indonesia: Java: Dieng Plateau.

Types. 3 male and 1 female syntypes, central Java, Dieng Plateau 2000 m, vi.1929, German limnological expedition (BMNH).

Other material examined. ***Indonesia.*** 1 male, Java occ., S. Papandaian, 4.iv.1931, 2400 m, F.W.F. (sub *megacephalus* Gschw., det. Gschwendtner) (OLML); 14, Java, Dieng area, J20, 30.i.1987, M.A. Jäch (NMW, cGG, cLH).

Diagnosis. ***Length.*** 3.1–3.5 mm. ***Habitus.*** As in *A. bistrigatus*. See Fig. 1. This species is extremely similar to *A. bistrigatus* (see the description by Watts 1978; the description above). The differences we found are a keel-like upfolding of the anterior third of the suture of the postcoxal processes, which is present in the male of *A. thienemanni*. In *A. bistrigatus*, the postcoxal process is smooth medially in both sexes. The elytron of *A. thienemanni* is more or less unicolour, not with darker patches, which are usually present in *A. bistrigatus*. The male appears shiny, the female dull due to shagreenation of the upper surface. In one specimen studied, the median lobe appears stouter than in *A. bistrigatus* (Fig. 3h), but in other specimens the form of the median lobe well agrees with the latter.

Distribution. Indonesia: Java (Fig. 6).

Habitat. Taken from a pond, and from a first order stream below a sulphur spring (Csiki 1938). Subsequently, the species was taken from swamps and a small lake (Telaga Warna) by M. Jäch, who assumes that the species must be extremely common (Jäch pers. comm. 2000). The studied sites are of volcanic origin.

Genus *Limbodessus* Guignot

Limbodessus Guignot 1939: 52.
Boongurrus Larson 1994: 217; **syn. n.**
Tjirtudessus Watts & Humphreys 1999: 122; **syn. n.**
Nirridessus Watts & Humphreys 1999: 124: Watts & Humphreys 2003, 136.

Type species. *Bidessus neoguinensis* Régimbart 1899 [*Hydroporus compactus* Clark 1862], by original designation (Guignot 1939: 52, see also Nilsson *et al*. 1989 and Nilsson 2001).

Remarks. Based on the molecular phylogenetic analyses of Cooper *et al*. (2002) and our results we synonymize *Boongurrus* and *Tjirtudessus* with *Limbodessus*. We also transfer all the Australian species of *Liodessus* to *Limbodessus.* This synonymy was foreshadowed by the morphological work of Larson (1994; original descr. of *Boongurrus*), Balke (2000), Watts & Humphreys (2003), as well as unpublished molecular work by Leys, Cooper and Watts (Watts, pers. comm. 2002). In fact, in the original description of *Tjirtudessus*, Watts & Humphreys 1999: 131 state: '[…] point quite strongly to a relationship to *Limbodessus*, *Liodessus* or *Boongurrus*, even though the new [genus] lack[s] a cervical stria [(see below)], identified by Biström (1988) to be a phylogenetically significant character in the Bidessini…'. Larson (1994) notes that *Boongurrus* keys to *Allodessus* plus *Liodessus* [represented by the American *L. affinis* Say] in the key provided by Biström (1988), and suggests that the main difference between *Boongurrus* and the other group of genera was the form of the paramere which is fingerlike in *Boongurrus* and longish in the others [the American *Liodessus*]. Interestingly, Larson also found that the Australian *Liodessus* differ from American and African *Liodessus* 'in having the apical paramere segment relatively short although its reflexed apical lobe is slender and finger-like. For this reason, the Australian clade of *Liodessus* is likely the sister taxon to *Boongurrus*' (Larson 1994: 221). There is no discussion of *Limbodessus*, and no justification for the proposed sister-group relationship of *Boongurrus* and the Australian *Liodessus*. There is also not a single apomorphy mentioned that would justify the description of the new genus *Boongurrus*. The same is true for *Tjirtudessus* (cf., Watts & Humphreys 1999).

Limbodessus is well characterised morphologically: All the species have a short, stout and hook-shaped distal end of the parameres (Biström 1988: 17; Larson 1994; Watts & Humphreys 1999, 2000, 2001, 2003; Balke 2000). This character does not occur in other Bidessini, except for a few African species of *Platydytes* Biström (1988) (Biström 1988; Larson 1994; Balke 2000). Thus, *Platydytes* may also be part of *Limbodessus*, a possibility that will be evaluated in detail in a future comprehensive analysis of Bidessini relationships. The paramere morphology of the 'true' *Liodessus (*type species: the American *Hydroporus affinis* Say 1823) differs remarkably, as the distal portion is long, with a short emargination at the tip (Biström 1988: 20). *Liodessus* is otherwise also known from Africa (Biström 1988). An unpublished molecular phylogenetic analysis of Dytiscidae (Ribera, Balke and Vogler) provides strong support for the non-monophyly of the Australian and American *Liodessus* and *Limbodessus*, which was also found by Leys, Cooper and Watts in their yet unpublished molecular phylogenetic analysis of Bidessini (Watts pers. comm. 2002).

Although *Limbodessus* is readily characterised morphologically, it is a rather diverse group with respect to habitats and structures. Species formerly assigned to *Liodessus,* as well as *Limbodessus compactus,* are 'normal' surface water Bidessini with well developed eyes and wings (some former '*Liodessus'* are also found in the hyporheic interstitial (Watts and Leys, pers. comm. 2002). '*Boongurrus'* exclusively inhabit the hyporheic interstitial and it is interesting to note that their eyes are relatively small (Larson 1994), but the wings are fully developed. '*Tjirtudessus'* includes rather unpigmented groundwater species with either remnant, but usually reduced eyes and reduced wings (Watts & Humphreys 1999; 2003). Finally, there are several undescribed subalpine species from the New Guinea highlands (2800–4000 m altitude, species 'r' and 'g' in Cooper *et al*. 2002 and our Fig. 1) that are strongly pigmented, almost black and wingless, some of them with a conspicuously cordiform pronotum (Balke 2000; Balke & Nilsson unpubl. data 2003).

Important characters for previous Bidessini classification were the presence or absence of (1) a line connecting the hind angles of the eyes ('occipital line', 'cervical line') (2) a basal epipleural pit posteriorly delimited by a carina, and (3) a short longitudinal cut at the base of the elytron ('elytral stria') (Biström 1988). Different combinations of these characters were previously used to define genera. However, characters (1) and (3) are highly homoplastic. For example, Larson (1994) observes a weak or absent cervical line on different specimens of *Boongurrus rivulus*, which means that different specimens of the same species would have to be assigned to different genera accepting the previously believed 'high phylogenetic value' of this character. In closely related New Guinea high-altitude species, characters (1) and (3) may be present or absent or faint in different species/specimens (Balke & Nilsson unpubl. data 2003).

The main argument for the description of *Boongurrus* was that it looks different from *Liodessus* (Larson 1994), and the rationale for erecting *Tjirtudessus* was the lack of a cervical line, thus being different from *Boongurrus*, *Liodessus* and *Limbodessus* (Watts & Humphreys 1999). We suggest that deviating morphologies here reflect morphological adaptations to different habitats, rather than deviating phylogenies. Balke *et al*. (2004) demonstrated that especially in the case of species with 'aberrant' ecological strategies it is advisable to carefully search for close relatives, rather than new genera.

Within the clade comprising *Allodessus* and *Limbodessus* character (2) is only present in *Limbodessus compactus*, suggesting independent origin of this feature here, and not suggesting a close relationship with other Bidessini, which have this basal epipleural carina such as *Clypeodytes* Régimbart (see also Fig. 1 for rejection of a close relationship, also Cooper *et al*. 2002).

A key to stygobiont *Limbodessus* was provided by Watts & Humphreys (2003), and a key to Australian epigean and hyporheic *Limbodessus* will be published later by Watts and Leys.

Checklist of *Limbodessus*

Oceania
L. cheesmanae (Balfour-Browne 1939) [Vanuatu], **n. comb.** (*Bidessus* Sharp)
L. curviplicatus (Zimmermann 1927[Samoa], **n. comb.** (*Bidessus*)
? Bidessus fijiensis (Balfour-Browne 1944) [Fiji] (only females known, but this species is similar to other *Limbodessus*)
Australia
Epigean
L. amabilis (Clark 1862), **n. comb.** (*Hydroporus* Clairville)
L. dispar (Sharp 1882), **n. comb.** (*Bidessus*)
L. gemellus (Clark 1862), **n. comb.** (*Hydroporus*)
L. inornatus (Sharp 1882), **n. comb.** (*Bidessus*)
L. praelargus (Lea 1899), **n. comb.** (*Bidessus*)
L. shukhardii (Clark 1862), **n. comb.** (*Hydroporus*)
?Hyporheic
L. rivulus (Larson 1994), **n. comb.** (*Boongurrus* Larson)
Stygobiont
L. bialveus (Watts & Humphreys 2003), **n. comb.** (*Tjirtudessus*)
L. bigbellensis (Watts & Humphreys 2000), **n. comb.** (*Nirridessus*)
L. challaensis (Watts & Humphreys 2001), **n. comb.** (*Nirridessus*)
L. cueensis (Watts & Humphreys 2000), **n. comb.** (*Nirridessus*)
L. cunyuensis Watts & Humphreys (2003), **n. comb.** (*Tjirtudessus*)
L. eberhardi Watts & Humphreys (1999), **n. comb.** (*Tjirtudessus*)
L. fridaywellensis (Watts & Humphreys 2001), **n. comb.** (*Nirridessus*)
L. hahni (Watts & Humphreys 2000), **n. comb.** (*Tjirtudessus*)
L. hinkleri (Watts & Humphreys 2000), **n. comb.** (*Nirridessus*)
L. jundeeensis (Watts & Humphreys 2003), **n. comb.** (*Tjirtudessus*)
L. karalundiensis (Watts & Humphreys 2003), **n. comb.** (*Tjirtudessus*)
L. lapostaae (Watts & Humphreys 1999), **n. comb.** (*Nirridessus*)
L. macrotarsus (Watts & Humphreys 2003), **n. comb.** (*Tjirtudessus*)
L. magnificus (Watts & Humphreys 2000), **n. comb.** (*Tjirtudessus*)
L. masonensis (Watts & Humphreys 2001), **n. comb.** (*Nirridessus*)
L. morgani (Watts & Humphreys 2000), **n. comb.** (*Nirridessus*)
L. pinnaclesensis (Watts & Humphreys 2001), **n. comb.** (*Nirridessus*)
L. pulpa (Watts & Humphreys 1999), **n. comb.** (*Nirridessus*)
L. raesidensis (Watts & Humphreys 2001), **n. comb.** (*Tjirtudessus*)
L. silus (Watts & Humphreys 2003), **n. comb.** (*Tjirtudessus*)
L. sweetwatersensis (Watts & Humphreys 2003), **n. comb.** (*Tjirtudessus*)
L. wilunaensis (Watts & Humphreys 2003), **n. comb.** (*Tjirtudessus*)
L. windarraensis (Watts & Humphreys 1999), **n. comb.** (*Nirridessus*)
L. yuinmeryensis (Watts & Humphreys 2003), **n. comb.** (*Tjirtudessus*)

Papuadessus pakdjoko Balke (Fig. 7a–e)

Papuadessus pakdjoko Balke 2001: 108.
Material examined. ***Papua New Guinea.*** 20, Simbu Province, Crater Mountain Wildlife Management Area, between Haia and Wara Sera, Oh River, 500 m, 12.ix.2002, M. Balke & K. Sagata (will be deposited in the University of Papua New Guinea, BMNH, NMW).
Notes. This species has been described from West New Guinea. Here we provide the first record from Papua New Guinea: A specimen from this series was used for sequencing here.

In addition to the description by Balke (2001), we provide additional SEMs here to illustrate surface sculpture and structure of this species (Fig. 7a–e).

DISCUSSION

Our phylogenetic analyses clearly support a monophyletic lineage, including all the species in our redefined *Allodessus* and

Limbodessus that were previously thought to belong to six disparate genera: *Tjirtudessus*, *Boongurrus*, *Limbodessus*, *Liodessus*, *Bidessus* and *Allodessus*. From a taxonomic point of view, the alternatives were either to consider the whole lineage a single genus, or to try to define monophyletic lineages within this clade that could stand as separate genera. Our decision was based on three main criteria: (1) within the species of the whole group there are clearly two types of male parameres, which agree with monophyletic groups found in the molecular phylogeny and thus are potential synapomorphies of the respective clades; (2) the two clades are supported in the trees considered optimal in all the analyses with the combined data; and (3) the name *Allodessus* is maintained for a highly supported and characteristic monophyletic lineage, thus favouring stability. The main consequence of our redefinition of the genus *Limbodessus* is the subordination within it of the large radiation of stygobiont Australian Bidessini (Watts & Humphreys 1999, 2003), with the only possible exception of the genus *Kitingka*, for which no molecular data are available (Cooper *et al*. 2002) and which might not even be a Bidessini. The highly modified morphology of the stygobiont species makes it difficult, if not impossible, to establish their phylogenetic relationships, and justifies their inclusion in newly created genera when no other data are available. However, when their relationships can be established (in our case with molecular data and characters of the genitalia), the taxonomy should be modified to favour the recognition of monophyletic taxa.

The genus *Allodessus*, which was previously thought to be a monospecific, typical Australian group, now is recognised to have a wide geographical range. Its five species, which previously had taxonomically uncertain positions, have here been proposed as a monophyletic group of closely related species. In fact, some of them may even prove to be conspecific, i.e., *A. bistrigatus*, *A. oliveri* and *A. thienemanni*, whereas at least some of the Tonga specimens attributed to *A. bistrigatus* may perhaps belong to a different species.

The distribution of *Allodessus* species (Fig. 6) is enigmatic and rather discontinous, with one species occurring only on a remote island (*A. skottsbergi*), one on a remote island as well as mainland New Zealand (*A. oliveri*), one species with a small range in the east Palearctic (*A. megacephalus*), one species only known from central Java (*A. thienemanni*) and one species with a wider range in Australia plus Tonga

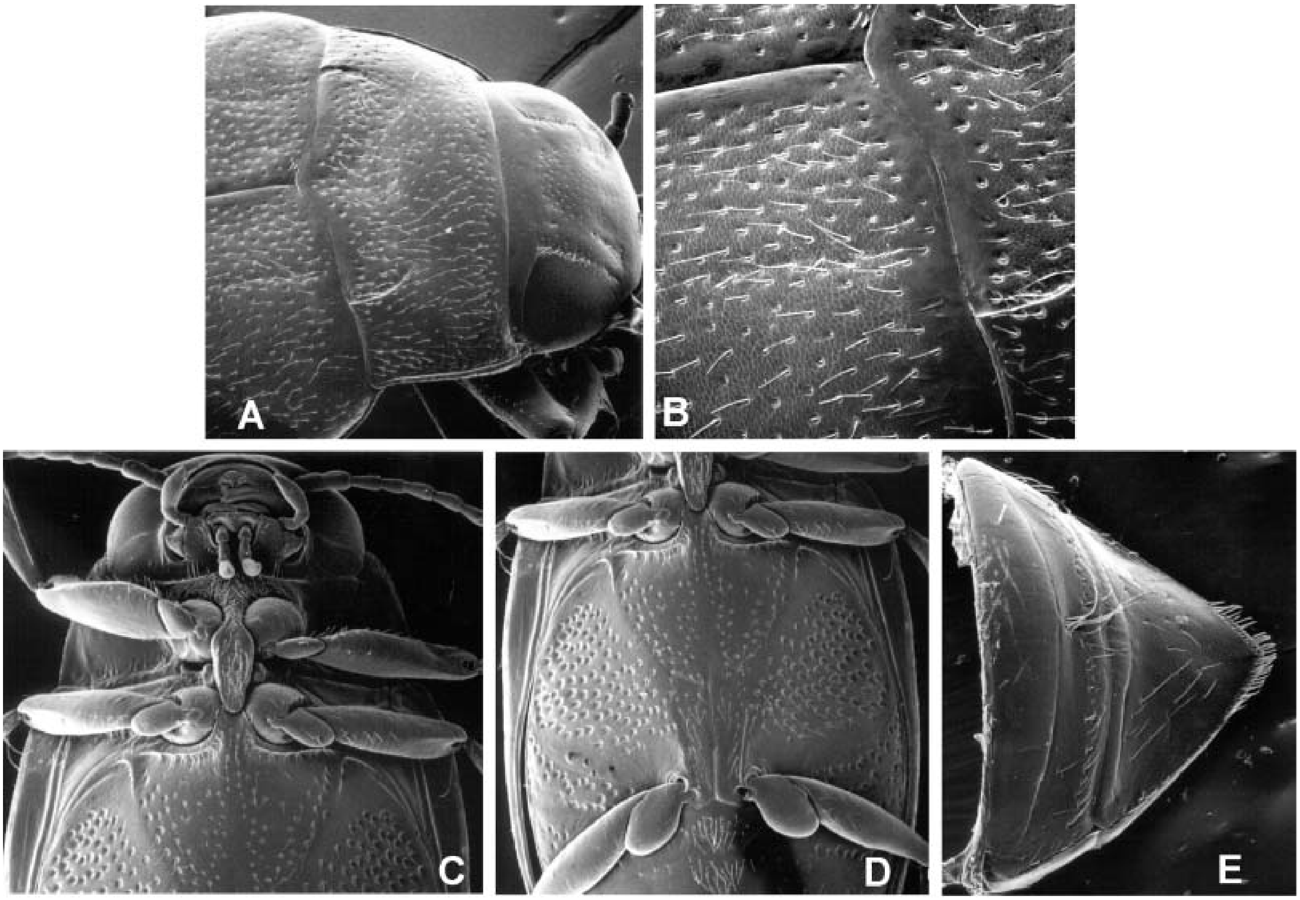

Fig. 7. *Papuadessus pakdjoko*, female: (a) head, pronotum and base of elytron in a dorsolateral view; (b) base of elytron, elytral suture, and base of pronotum, same view; (c) ventral aspect of head, prosternum and metaventrite; (d) ventral aspect mainly showing metaventrite and metacoxae; (e) sternites VI and VII.

(*A. bistrigatus*). Species of *Allodessus* have not yet been reported from the vast areas between the ranges of the different taxa, including New Guinea and New Caledonia, where huge collections of Dytiscidae have been made. The range of the species of *Allodessus* suggests that the species are strong dispersers, as Australia and Asia have never been connected by dry corridors. The same is true for the Kermadec and Easter Islands, which always were separated from other land masses.

Previously *Limbodessus* was believed to be monospecific and rather widespread in Japan, south-east Asia and the Australian region (Balke & Satô 1995). Here we suggest that the group has radiated extensively in the Australian region. Based on the analysis of Cooper *et al*. (2002) and our analyses we speculate that one species, *L. compactus*, may have dispersed widely from Australia into the Oriental and Eastern Palaearctic regions.

Biogeographical boundaries such as Wallace's line (Fig. 6), which have been postulated in the transition zone between Asia and Australia in abundance (see, e.g., van Oosterzee 1997) have not much affected the range of *Allodessus* and *Limbodessus* species, which are obviously able to cope with a variety of climatic regimes. Widespread dispersal in this group of beetles is yet another factor that confuses biogeographical patterns in the megadiverse zone spanning from Asia to Australia, puzzling biogeographers ever since Wallace (1860).

ACKNOWLEDGEMENTS

We thank Dr Martin Baehr (Munich), Mag. F. Gusenleitner (Linz), Dr Ricardo Palma (Wellington), Dr G.A. Samuelson (Honolulu), Dr S. Thorpe (Auckland) and Prof Dr Günther Wewalka (Vienna) for loan of specimens, and Katayo Sagata (Goroka, Papua New Guinea) and Chris Watts (Adelaide) for help in the field. Thanks to Chris Watts (Adelaide) and three referees for useful comments on the manuscript. MB thanks the Natural History Museum Vienna, the Erich Kirschenhofer Foundation (Vienna), and the IHP program of the European Community for financial support. Thanks are also due to Dr Paul J. Spangler for his help during the stay of MB at the Smithsonian Institution in Washington that was funded by the Smithsonian Office of Fellowships and Grants (OFG). This research has been supported by the Linnean Society of London and a Marie Curie Fellowship of the European Community programme to MB, IHP (IHP-MCFI-99–1) under contract number HPMF-CT-2001–01365. IR was supported by a Leverhulme Special Research fellowship.

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Accepted for publication 8 September 2003.