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A first broad-scale molecular phylogeny of Prionoceridae (Coleoptera: Cleroidea) provides insight into taxonomy, biogeography and life history evolution

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Abstract

Based on partial sequences of three mitochondrial (*cox1*, *cox2*, *trnL*) and two nuclear genes (*18S* and *28S*) we conducted a molecular phylogenetic analysis of Prionoceridae represented by all three valid genera, 34 species and a large number of informal species groups from the Palaearctic, Afrotropical and Oriental regions. Analyses indicate the split of Prionoceridae in two main clades, Lobonychinae and Prionocerinae. Lobonychinae includes the genus *Lobonyx* Jacquelin du Val, 1859 and some species currently placed in *Idgia* Laporte de Castelnau, 1838. Prionocerinae includes a large paraphyletic grade of *Idgia* and monophyletic *Prionocerus* Perty, 1831, with *Idgia virides-cens* Gorham, 1895 identified as a sister group to *Prionocerus*. *Idgia* consists of seven clades, with their basal relationships weakly resolved. Two clades – *Idgia oculata* and *Idgia pallidicolor* species groups – are well supported by molecular data and morphological characters. Species identifications based on morphology are consistent with tree topology recovered from molecular dataset, with one possible exception (*Idgia inapicalis*). Sequence divergence in *cox1* varies from 3.7 to 16% between species and from 0 to 4.9% within species of Prionoceridae. The reconstruction of diurnal and nocturnal life histories suggests a single origin of nocturnality, and multiple transitions from nocturnal to diurnal life style within Prionoceridae. The African and the Arabian species represent two lineages, both having their origin in tropical Asia.

Key words

Soft-winged flower beetles, Cucujiformia, *Idgia*, *Prionocerus*, *Lobonyx*, taxonomy, nocturnality, diurnality, biogeography, barcoding.

1. Introduction

Molecular systematic methods are of increasing importance in building the "Beetle Tree of Life". An important first step towards this goal has been the paper of Hunt et al. (2007), examining higher-level phylogeny within the whole Coleoptera based on three partial gene sequences. The majority of beetle families, however, have never been subject to a detailed phylogenetic analysis.

Prionoceridae is a poorly known family within the melyrid lineage ("soft-winged flower beetles") of the superfamily Cleroidea (Polyphaga: Cucujiformia). Formerly, prionocerid beetles were placed in the superfamily "Malacodermata", assuming a relationship with Cantharidae (soldier beetles), as both have a very similar external appearance (Lacordaire 1857). However, based on larval (Böving & Craighead 1931) and adult characters (Crowson 1955), the Melyridae lineage was later shown to be closely related to other groups, e.g. Cleridae and Trogossitidae. Once the Malacodermata was split into superfamilies Cantharoidea (now part of Elateroidea) and Cleroidea, Prionoceridae was formally placed in Cleroidea and treated as either a subfamily of Melyridae in the wider sense (Crowson 1955; Majer 1987), or as

a separate family (MAJER 1994; LAWRENCE & NEWTON 1995). The apparent morphological similarity of prionocerids and cantharids is probably due to convergent life histories (CROWSON 1964). Recently, the phylogeny of the Melyridae lineage of Cleroidea was examined in detail, based on molecular data of two ribosomal and two nuclear gene fragments (BOCAKOVA et al. 2012). Their analysis showed Melyridae s.lat. (the melyrid lineage) to consist of six clades, which were given family status and showed the following relationships: Rhadalidae + (Mauroniscidae + (Prionoceridae + (Melyridae s.str. + (Dasytidae + Malachiidae)))). These groupings are largely consistent with morphological data (MAJER 1994) and with the previous, large-scale molecular phylogenetic analysis of the whole Coleoptera (HUNT et al. 2007). However, these studies included only a small number of taxa within the Melyridae lineage. The BOCAKOVA et al. (2012) and HUNT et al. (2007) analyses provide the first glimpses of the phylogenetic relationships of Prionoceridae, but much remains to be understood of the generic and species level relationships.

Data on the biology of Prionoceridae is very scarce, with only a few aspects known from available literature, specimen label data and unpublished fieldwork experience. Like in other beetle families with weakly sclerotised cuticle ("malacoderms", e.g. Malachiidae and Cantharidae), adults of Prionoceridae are short lived and seasonally limited in their occurrence. They can be found in abundance locally, sometimes being among the most common and conspicuous insects, but tend to "disappear" after only a few days. Adults of diurnal species are flower visitors and probably all pollen feeders. Nocturnal species, possibly all of the yellow-coloured species of *Idgia*, have only been observed sitting motionless on the underside of leaves in forests or were attracted to light traps, without any data on their feeding behaviour. Larvae were found either under the bark of trees, or moving around on foliage of forest under-storey shrubs during rainy weather. They are either predators or feed on dead insects (saprophagous) (GARDNER 1929).

The vast majority of Prionoceridae species occur in the Oriental region, a minority in the Afrotropical and Palaearctic regions and only two widespread species reach parts of the Australian region. There are none on the Australian mainland, Madagascar and in the New World. Most Prionoceridae species are associated with tropical and subtropical moist forests, but the few Palaearctic taxa are recorded from drier, savannah-like habitats, dry temperate climates (Mediterranean, Central Asia), or from dry scrublands of the Arabian Peninsula.

Currently, Prionoceridae consists of 158 described species, placed in three poorly defined genera, *Prionocerus* Perty, 1831 (8 species), *Idgia* Laporte de Castelnau, 1838 (139 species) and *Lobonyx* Jacquelin du Val, 1859 (11 species). Based on a study of type material and museum collections worldwide, an additional 100+ undescribed species have been detected so far (M. Geiser, unpublished data). The internal phylogeny of Prionoceridae has never been subject to a detailed examination, and the generic placement of most taxa has not been under scrutiny since the last (partial) revision of *Idgia* and *Prionocerus* (CHAMPION 1919). Phylogenetic data are currently limited to a morphological study of Melyridae s.lat., including three prionocerid species (MAJER 1987), and the data recently provided by BOCAKOVA et al. (2012), which was limited to four species. Furthermore, some remarks on species placements and genus-level morphology were made in older works (CHAMPION 1919; CROWSON 1964), and in recent revisions of *Prionocerus* (GEISER 2010) and the East Palaearctic members of *Lobonyx* (CONSTANTIN 2009).

Using a dense sampling across the whole range of the family, this study aims to examine phylogenetic relationships of Prionoceridae. Using a molecular phylogenetic approach we aim to test the monophyly of genera and a number of informal species groups. These species-groups became apparent during morphological examination of over 200 prionocerid morphospecies. All species groups are named in this study for the first time – no names existed previously in the literature. We have given them "informal-names" to further understanding of these potential taxonomic groups of uncertain rank. Further, the biogeography of Prionoceridae is examined using a reconstructed phylogeny. These biogeographical categories reflect both traditional biogeographic regions but are more restrictive in cases because our sampling is limited. Additionally, the phylogeny provides an insight into the evolution of different life-history strategies. Interestingly, Prionoceridae includes a number of nocturnal species, which is unusual within the melyrid lineage. Morphological characters associated with nocturnal life style include very large eyes and a dark or pale testaceous body colouration. Diurnal species, on the other hand, tend to have a bright metallic colouration and smaller eyes. As few data is known on the behaviour, certain morphological characteristics can be used to infer behaviour. Our phylogeny provides a means to test the evolution of diurnality and nocturnality in prionocerids.

2. Material and methods

2.1. Data and taxon sampling

Previous sequencing efforts within the melyrid clade of Cleroidea was limited to the studies of BOCAKOVA et al. (2012), HUNT et al. (2007), HUNT & VOGLER (2008) and LEVKANICOVA (2009), who provided a number of cytochrome oxidase subunit I (*cox1*; mitochondrial), 16S rRNA (*16S*; mitochondrial), 18S rRNA (*18S*; nuclear) and 28S rRNA (*28S*; nuclear) sequences in their analyses. Data for *cox1* (13 sequences), *18S* (14 sequences) and *28S* (11 sequences), representing a total of six Prionoceridae species and nine species from other Cleroidea taxa were used in this study (see Table 1). Our own sequencing programme added 70 *cox1*, 24 *18S* and seven

Table 1. Previously known partial gene sequences used in the present study, including their GenBank accession numbers, voucher numbers, country of origin (if known) and literature reference(s). Voucher specimens of Prionoceridae species were revised and re-identified by the first author: "*Idgia* sp. UPOL ZL0103" in GenBank corresponds to *I. pallidicolor*, while "*Idgia* sp. 1217" corresponds to *I.* cf. *subcostulata*.

Species	Family	Voucher	cox1	18S	28S	Country	Reference
Idgia cf. *subcostulata* Pic, 1910	Prionoceridae	UPOL001217	HQ619630	HQ619497	HQ619565	Indonesia	Bocakova et al. 2012
Idgia cincta Pic, 1906	Prionoceridae	UPOL001090		EF209686	HQ619519	Indonesia	Hunt et al. 2007; Bocakova et al. 2012
Idgia pallidicolor Pic, 1906	Prionoceridae	UPOL ZL0103	EF490187	EF209685	FJ903952	Indonesia	Hunt et al. 2007; Bocakova et al. 2012; Levkanicova 2009
Idgia sp.	Prionoceridae	BMNH668224		DQ337165			Hunt & Vogler 2008
Lobonyx aeneus (Fabricius, 1798)	Prionoceridae	UPOL001086	EF508052	EF209687	HQ619517	Morocco	Hunt et al. 2007; Bocakova et al. 2012
Prionocerus bicolor Redtenbacher, 1868	Prionoceridae	UPOL001216	HQ619629	HQ619496	HQ619564	Indonesia	Bocakova et al. 2012
Dasytidius gracilis Escalera, 1914	Dasytidae	UPOL001069	EF508049	EF209712	HQ619506	Morocco	Hunt et al. 2007; Bocakova et al. 2012
Dasytes aeratus Stephens, 1829	Dasytidae	UPOL001066	HQ619570	EF209709	HQ619503	Czech Republic	Hunt et al. 2007; Bocakova et al. 2012
Danacea nigritarsis (Küster, 1850)	Dasytidae	UPOL001064	EF508048	EF209707	HQ619502	Czech Republic	Bocakova et al. 2012
Anthocomus rufus (Herbst, 1784)	Malachiidae	BMNH679272	DQ221960	AY748136			Hunt & Vogler 2008
Amecomycter rugicollis Majer, 1995	Mauroniscidae	UPOL001183	HQ61961	HQ619487	HQ619555	Chile	Bocakova et al. 2012
Falsomelyris granulata (Fabricius, 1792)	Melyridae	UPOL001077	EF508051	EF209700	HQ619511	Morocco	Hunt et al. 2007; Bocakova et al. 2012
Aplocnemus perforatus Schilsky, 1897	Rhadalidae	UPOL001073	EF508050	EF209702	HQ619509	Morocco	Bocakova et al. 2012
Necrobia rufipes (DeGeer, 1775)	Cleridae	UPOL001135	EF508057	EF209698		Japan	Hunt et al. 2007
Ostoma ferruginea (Linnaeus, 1758)	Trogossitidae	BMNH679285	DQ222026	AY748138	DQ202661		Hunt & Vogler 2008

Table 2. List of DNA samples and their corresponding voucher specimens presented in the current study. Collecting localities and future depositories are given for each specimens. GenBank reference numbers for each available sequence are indicated (*cox2* and *trnL* share the same GenBank record with their respective *cox1* sequence). DNA-VN = DNA voucher number.

Species	DNA-VN	Depository	Country	Locality	cox1	18S	28S	trnL	cox2
Idgia arabica Champion, 1919	A324	NMPC	Yemen	Sanaa	KF703683	KF703715	KF703691	KF703683	KF703683
Idgia caeruleiventris Champion, 1919	A220	BMNH	Malaysia	Pahang, Tanah Rata	KF703675	KF703711			
Idgia cf. *subcostulata* Pic, 1910	A196	BMNH	Indonesia	Sumatra, Kersik Tua, Gunung Kerinci	KF703665			KF703665	KF703665
Idgia cyanocephala Champion, 1919	A135	BMNH	Malaysia	Pahang, Tanah Rata	KF703623	KF703695		KF703623	
Idgia cyanocephala Champion, 1919	A165	BMNH	Malaysia	Pahang, Tanah Rata	KF703642				
Idgia flavicollis Redtenbacher, 1868	A199	BMNH	China	Hong Kong	KF703667	KF703709	KF703689		
Idgia flavirostris Pascoe, 1860	A183	NMPC	China	Jiangxi, Jinggang Shan, Xiangzhou	KF703653			KF703653	KF703653
Idgia flavirostris Pascoe, 1860	A185	NMPC	China	Jiangxi, Jinggang Shan, Baiyinhu	KF703655	KF703706		KF703655	
Idgia flavirostris Pascoe, 1860	A188	NMPC	China	Jiangxi, Jinggang Shan, Xiaoxidong	KF703657			KF703657	KF703657
Idgia flavirostris Pascoe, 1860	A201	BMNH	China	Hong Kong	KF703669			KF703669	KF703669
Idgia flavirostris Pascoe, 1860	A204	BMNH	China	Hong Kong	KF703671			KF703671	KF703671
Idgia flavirostris Pascoe, 1860	A206	BMNH	China	Hong Kong	KF703673				
Idgia fulvicollis Reiche, 1849	A119	BMNH	Ethiopia	Sidamo, Yabelo	KF703619	KF703694	KF703686		
Idgia fulvicollis Reiche, 1849	A152	BMNH	Ethiopia	Sidamo, Yabelo	KF703637			KF703637	KF703637
Idgia fulvicollis Reiche, 1849	A195	BMNH	Ethiopia	Sidamo, Yabelo	KF703664			KF703664	KF703664
Idgia inapicalis Pic, 1910	A221	NHMB	Malaysia	Pahang, Tanah Rata	KF703676				
Idgia inapicalis Pic, 1910	A326	BMNH	Indonesia	Sumatra Barat, Lake Maninjau, E coast	KF703684				
Idgia cf. *inapicalis* Pic, 1910	A139	BMNH	Indonesia	Sumatra, Brastagi, Gunung Sibayak	KF703625	KF703696		KF703625	KF703625
Idgia maculatithorax Pic, 1919	A116	NHMB	Laos	Xieng Khouang, Phou Sane	KF703616	KF703692	KF703685	KF703616	KF703616
Idgia maculatithorax Pic, 1919	A134	NHMB	Laos	Xieng Khouang, Phou Sane	KF703622			KF703622	

Table 2 continued.

Species	DNA-VN	Depository	Country	Locality	cox1	18S	28S	trnL	cox2
Idgia maculatithorax Pic, 1919	A155	NHMB	Laos	Xieng Khouang, Phou Sane	KF703640			KF703640	KF703640
Idgia maculatithorax Pic, 1919	A194	NHMB	Laos	Xieng Khouang, Phou Sane	KF703663			KF703663	KF703663
Idgia oculata Redtenbacher, 1868	A200	BMNH	China	Hong Kong	KF703668			KF703668	KF703668
Idgia oculata Redtenbacher, 1868	A203	BMNH	China	Hong Kong	KF703670			KF703670	KF703670
Idgia particularipes Pic, 1920	A207	NHMB	Laos	Xieng Khouang, Ban Thachok	KF703674	KF703710		KF703674	KF703674
Idgia setifrons (Kirsch, 1875)	A322	BMNH	Malaysia	Sabah, Sepilok	KF703681	KF703713	KF703690	KF703681	KF703681
Idgia varicornis Champion, 1919	A178	NHMB	Laos	Bokeo, Nam Kan NPA, 5 km W Ban Toup	KF703649	KF703703		KF703649	KF703649
Idgia viridescens Gorham, 1895	A145	BMNH	India	Himachal Pradesh, Solan, Sallagat	KF703630	KF703698			
Idgia n.sp.1 (Yunnan, Laos)	A173	NHMB	China	Yunnan, Xishuangbanna, Menglun	KF703644	KF703701		KF703644	KF703644
Idgia n.sp.1 (Yunnan, Laos)	A189	NHMB	Laos	Bokeo, Nam Kan NPA, 5 km W Ban Toup	KF703658			KF703658	KF703658
Idgia n.sp.2 (Laos)	A150	NHMB	Laos	Xieng Khouang, Ban Thaviang	KF703635			KF703635	KF703635
Idgia n.sp.2 (Laos)	A176	NHMB	Laos	Bolikhamxay, Nam Kading NPA, Tad Paloy	KF703647			KF703647	KF703647
Idgia n.sp.2 (Laos)	A180	NHMB	Laos	Bokeo, Nam Kan NPA, 5 km W Ban Toup	KF703651			KF703651	KF703651
Idgia n.sp.3 (Laos)	A151	NHMB	Laos	Xieng Khouang, Phou Sane	KF703636	KF703700		KF703636	KF703636
Idgia n.sp.4 (Laos)	A182	NHMB	Laos	Savannakhet, Phou Xang He	KF703652	KF703705	KF703687	KF703652	KF703652
Idgia n.sp.4 (Laos)	A190	NHMB	Laos	Savannakhet, Phou Xang He	KF703659			KF703659	KF703659
Idgia n.sp.5 (Sabah)	A320	BMNH	Malaysia	Sabah, Kinabalu NP, headquarters	KF703679			KF703679	KF703679
Idgia n.sp.6 (Sabah)	A321	BMNH	Malaysia	Sabah, Kinabalu NP, headquarters	KF703680	KF703712		KF703680	KF703680
Idgia n.sp.7 (Sabah)	A323	BMNH	Malaysia	Sabah, Danum Valley	KF703682	KF703714		KF703682	KF703682
Idgia n.sp.8 (Kalimantan)	A192	BMNH	Indonesia	Central Kalimantan, Sungei Mohot, Murung Raya	KF703661	KF703708	KF703688	KF703661	KF703661
Idgia n.sp.9 (Mindanao)	A148	BMNH	Philippines	Mindanao, Mt. Apo, L. Agco	KF703633	KF703699		KF703633	KF703633
Idgia n.sp.10 (Mindanao)	A205	BMNH	Philippines	Mindanao, Mt. Apo, L. Agco	KF703672				
Idgia n.sp. near *granulipennis* (Yunnan)	A175	NHMB	China	Yunnan, Gaoligongshan, 50 km E Tengchong	KF703646	KF703702		KF703646	KF703646
Idgia n.sp. near *granulipennis* (Yunnan)	A191	NHMB	China	Yunnan, Gaoligongshan, 50 km E Tengchong	KF703660			KF703660	KF703660
Idgia sp. (Sumatra)	A163	NHMB	Indonesia	Sumatra, Kersik Tua, Gunung Kerinci	KF703641				
Prionocerus bicolor Redtenbacher, 1868	A115	NHMB	Laos	Xieng Khouang, Phonsavan	KF703615				
Prionocerus bicolor Redtenbacher, 1868	A117	NHMB	Laos	Xieng Khouang, Phonsavan	KF703617				
Prionocerus bicolor Redtenbacher, 1868	A132	NHMB	Laos	Champasak, Muang Paksong	KF703620				
Prionocerus bicolor Redtenbacher, 1868	A146	NHMB	Laos	Xieng Khouang, Phonsavan	KF703631			KF703631	KF703631
Prionocerus bicolor Redtenbacher, 1868	A149	NHMB	Laos	Champasak, Ban Nong Panouan	KF703634			KF703634	KF703634
Prionocerus bicolor Redtenbacher, 1868	A154	NHMB	Laos	Xieng Khouang, Phonsavan	KF703639			KF703639	KF703639
Prionocerus bicolor Redtenbacher, 1868	A172	NHMB	Laos	Attapeu, Ban Vang Tat Noi	KF703643			KF703643	KF703643
Prionocerus bicolor Redtenbacher, 1868	A177	NHMB	Laos	Louang Namtha, Muang Sing	KF703648			KF703648	KF703648

Table 2 continued.

Species	DNA-VN	Depository	Country	Locality	cox1	18S	28S	trnL	cox2
Prionocerus bicolor Redtenbacher, 1868	A184	NHMB	Laos	Savannakhet, Ban Pa Phaknau	KF703654			KF703654	KF703654
Prionocerus bicolor Redtenbacher, 1868	A193	NHMB	Laos	Savannakhet, Ban Pa Phaknau	KF703662			KF703662	KF703662
Prionocerus coeruleipennis Perty, 1831	A118	NHMB	Laos	Vientiane, Ban Hin Ngon	KF703618	KF703693			
Prionocerus coeruleipennis Perty, 1831	A133	NHMB	Laos	Xieng Khouang, Phonsavan	KF703621			KF703621	KF703621
Prionocerus coeruleipennis Perty, 1831	A138	BMNH	Philippines	Mindanao, Mt. Malindang	KF703624			KF703624	KF703624
Prionocerus coeruleipennis Perty, 1831	A141	NHMB	Laos	Xieng Khouang, Ban Thaviang	KF703627			KF703627	KF703627
Prionocerus coeruleipennis Perty, 1831	A143	NHMB	Laos	Louang Prabang, Muang Phou Khoune	KF703628			KF703628	KF703628
Prionocerus coeruleipennis Perty, 1831	A147	NHMB	Laos	Xieng Khouang, Ban Na Lam	KF703632			KF703632	KF703632
Prionocerus coeruleipennis Perty, 1831	A174	NHMB	Laos	Louang Namtha, Muang Sing	KF703645			KF703645	KF703645
Prionocerus coeruleipennis Perty, 1831	A197	NHMB	Laos	Louang Prabang, Thong Khan	KF703666			KF703666	KF703666
Prionocerus n.sp.	A179	NMPC	China	Guangdong, Heishiding Nat. Res.	KF703650	KF703704		KF703650	KF703650
Prionoceridae gen.sp. larva	A144	NHMB	Laos	Bolikhamxay, Nam Kading NPA, Tad Paloy	KF703629	KF703697		KF703629	KF703629
Prionoceridae gen.sp. larva	A244	NHMB	Laos	Bokeo, Nam Kan NPA, 5 km W Ban Toup	KF703677			KF703677	KF703677
Prionoceridae gen.sp. larva	A245	NHMB	Laos	Khammouan, Nakai-Nam Theun NBCA, Ban Navang	KF703678			KF703678	KF703678
outgroup taxa:									
Spinapalochrus rufofasciatus Pic, 1919	A140	NHMB	Laos	Xieng Khouang, Phonsavan	KF703626			KF703626	KF703626
Omadius sp.	A153	NHMB	Laos	Houa Phan, Ban Saluei, Phou Pane	KF703638			KF703638	KF703638
Acanthocnemus nigricans (Hope, 1845)	A186	NHMB	Laos	Attapeu, Thong Kai Ohk, Ban Kachung	KF703656	KF703707		KF703656	KF703656

28S sequences, taken from 70 individuals representing 30 species of Prionoceridae (28 in addition to previous studies), as well as three other Cleroidea (outgroup) taxa and three larval specimens, the latter were not identifiable according to morphology (see Table 2). Taxon sampling within Prionoceridae covers all valid genera, of which *Prionocerus* and *Lobonyx* are represented by their respective type species (*P. coeruleipennis* and *L. aeneus*) and *Idgia* Laporte de Castelnau, 1838 is represented by a species, *I. fulvicollis*, suggested to be closely related to the type species, *I. terminata* Laporte de Castelnau, 1838. Outgroup taxa cover all major clades of Cleroidea, including all families treated by Bocakova et al. (2012), newly including Acanthocnemidae. All specimens used in this study, except one, were preserved in 96–100% ethanol prior to extraction. For *Idgia viridescens*, a recently collected dry prepared specimen was used.

A part of sequenced species has not yet been formally described. This is currently being established, based on a large-scale morphological revision of prionocerid type material and other museum specimens (M. Geiser, unpublished data). Two species remain unidentified, one of them cited by Hunt & Vogler (2008) under the name "Idgia sp. BMNH668224", of which the voucher specimen was not found at BMNH.

2.2. DNA extraction, amplification and sequencing

The chosen non-destructive extraction combines the protocol given by Gilbert et al. (2007) with standard extraction technique using an EZ1 DNA tissue extraction kit (QiaGen, Hilden, Germany). Whole specimens were incubated overnight in a buffer containing proteinase-K at 56°C after cutting open the membrane between pro- and mesothorax, in order to provide easier access to the thoracic muscle tissue. Voucher specimens were dry-mounted, labelled with voucher designation and stored for future reference in public museum collections (see Table 2), abbreviated as follows: BMNH = Natural History Museum, London, UK; NHMB = Naturhistorisches Museum, Basel, Switzerland; NMPC = Entomology Department, National Museum, Prague, Czech Republic.

Partial gene sequences for *cox1*, *18S* and *28S* were amplified using the primers reported by BOCAKOVA et al. (2012) and SHULL et al. (2001). For *cox1*, additional primers "Pat" and "Marilyn" (SIMON et al. 1994) were used, when amplification with the first set of primers failed. This set added an additional 64–318 *cox1* bp beyond the end of the *cox1* gene, representing the t-RNA-Leu (*trnL*) and the first portion of the cytochrome oxidase subunit II (*cox2*) genes. PCR conditions included the following steps: Initial denaturation for 1 min at 94°C, followed by 35 cycles of 1 min denaturation at 94°C; annealing for 1 min at 49–51°C; extension at 72°C for 90 sec and a final extension step for 7 min at 72°C.

CodonCode Aligner (CodonCode Corp., Centerville, MA, USA) and Geneious 5.5.6 (Biomatters Ltd., Auckland, New Zealand) were used for assembling chromatograms and sequence editing.

2.3. Sequence alignment and phylogenetic analyses

Edited and verified sequences were aligned using Geneious Pro (Biomatters Ltd.). Protein coding sequences (*cox1* and *cox2*) were partitioned into 1st, 2nd and 3rd codon position data using TranslatorX (www.translatorx.co.uk). Conserved blocks of rRNA markers (18S and 28S) were selected using less stringent settings in GBlocks version 0.91b (CASTRESANA 2000, 2002), while non-conserved gene fractions of unalignable variable length were discarded. Data were assigned to nine partitions, *18S*, *28S*, *trnL*, and the 1st, 2nd and 3rd codon position of *cox1* and *cox2* respectively. Best-fit models were estimated for each partition using Geneious Pro. We assessed saturation of each partition by plotting Jukes-Cantor p-distances (JUKES & CANTOR 1969) against HKY85 distances (HASEGAWA, KISHINO & YANO 1985). Data that showed saturation (non-linear relationship) were excluded from the analysis {9}.

Phylogenetic tree searches were performed from these alignments using three main approaches, Bayesian Inference (BI; HUELSENBECK et al. 2001), Maximum Likelihood (ML; FELSENSTEIN 1981) and Parsimony (PA). In order to balance incomplete species sampling against missing data for some genes, different data matrices were analysed, with variable coverage of species and amounts of missing sequence data.

For the phylogenetic analyses, nine datasets were produced, each with a different set of samples and/or sequences:

{1} *cox1*, *18S* and *28S* sequences (3156 bp in total) from 18 samples representing 12 Prionoceridae (representing major clades) and 6 outgroup species [no missing data].

{2} *cox1* and *18S* sequences (2590 bp) from 38 samples representing 29 Prionoceridae (representing most of the included species) and 9 outgroup species [two taxa lacking *cox1* data].

{3} *cox1*, *cox2*, *trnL*, *18S* and *28S* sequences (i.e. all available gene fragments; 3522 bp) from 85 samples representing 34 Prionoceridae and 12 outgroup species [some missing data for all gene fragments except *cox1*].

{4} *cox1* sequences only (828 bp) from 82 samples representing 33 Prionoceridae and 12 outgroup species [no missing data].

{5} *18S* sequences only (1762 bp) from 38 samples representing 29 Prionoceridae and 9 outgroup species [no missing data].

{6} *28S* sequences only (566 bp) from 18 samples representing 12 Prionoceridae and 6 outgroup species [no missing data].

{7} *cox1*, *cox2*, *trnL* (i.e. all available mitochondrial gene fragments; 1147 bp) from 76 samples representing 32 Prionoceridae and 11 outgroup species [some missing data for *cox2* and *trnL*, but mostly in outgroup species].

{8} *18S* and *28S* (i.e. all available nuclear gene fragments; 2328 bp) from 38 samples representing 30 Prionoceridae and 8 outgroup species [some missing data for *28S*].

{9} Same as {3} but all potentially saturated DNA partitions excluded: *trnL* and 3rd codon positions of *cox1* and *cox2* (3086 bp).

BI analyses were performed on all datasets {1}–{9} using MrBayes version 3.2.1 (RONQUIST et al. 2012) running four simultaneous Markov chains for 5 million generations, sampling every 1000 generations, and discarding the first one million generations as burn-in to prevent sampling before reaching stationarity (Tracer v1.5; RAMBAUT & DRUMMOND 2007). Data were split in 9 partitions (see above), model parameters were independently optimized for each ("un-link" option in effect).

ML analyses were performed on datasets {1}–{3} (using RAxML 7.0.4: STAMATAKIS 2006). Data were split in 9 partitions (see above), model parameters were independently optimized for each ("un-link" option in effect).

PA analysis was performed on dataset {1}, the most parsimonious trees were calculated using PAUP 4.0b10 (SWOFFORD 1998), using a heuristic search option, with 100 random addition sequence replicates and tree bisection recombination branch swapping procedure.

Support for clades was evaluated for all approaches, for BI using posterior probabilities, for ML and PA non-parametric bootstrapping (FELSENSTEIN 1985) with 1000 replicates using (RAxML and PAUP 4.0b10). Furthermore, we calculated pairwise genetic distances for *cox1*, as these provide the largest sampling of taxa.

Ostoma ferruginea (Trogossitidae) was chosen to root BI, ML and PA trees, as it represents the most basally diverging member of Cleroidea included in the analyses of HUNT et al. (2007) and BOCAKOVA et al. (2012).

Further phylogenetic analyses were conducted to test whether a single origin of nocturnality within Prionoceridae was significantly different from optimal topologies. Species known or assumed to be nocturnal are listed in Table 4. We constructed a constraint showing all noctur-

nal species to be monophyletic and compared this tree with our optimal tree. As the life-history of *Idgia fulvicollis* is incompletely known, two different constraints were tested, assuming *Idgia fulvicollis*, to be either diurnal (constraint 1) or nocturnal (constraint 2). A putative relative of *Idgia fulvicollis* has been reported to be diurnal (REF). We constrained a tree using BI and PA approaches to test differences between topologies. For the PA, a non-parametric test (Templeton 1983) was used to assess the significance of length differences between most parsimonious and constraint trees. For BI, posterior probability values were compared qualitatively between constrained and optimal trees. Bayes Factors were calculated using Tracer v1.5 (Rambaut & Drummond 2007) to quantitatively test differences between optimal and constrained tree reconstructions. A log-Bayes Factor greater than 3 was considered as strong evidence in favour of the optimal hypothesis (Kass & Raftery 1995; Bergsten et al. 2013). Using BI reconstruction of dataset {3} we conducted an ancestral state reconstruction of life history modes in Prionoceridae using MESQUITE (Maddison & Maddison 2011). We applied two coding schemes for ancestral state reconstruction (see above) using the following coding (0 = diurnal, 1 = nocturnal). *Idgia fulvicollis* was scored as either nocturnal or diurnal, as the data are not clear for this particular species. There are, however, relatives of *I. fulvicollis* from the Afrotropical region, which are clearly diurnal (Marshall 1902).

To investigate area state reconstruction for areas we coded biogeographic areas (0 = Afrotropical, 1 = Arabia, 2 = Palaearctic (except Arabia), 3 = Indochina, 4 = Sundaland, 5 = Philippines and 6 = Himalayas) and scored them for all species, and reconstructed biogeographical relationships using MESQUITE (Maddison & Maddison 2011). Specimens collected in subtropical lowland areas of South China were coded as Indochinese, because at least one of the species, *I. oculata*, is distributed also in Vietnam (Yang et al. 2012). Species from high altitude localities in SW-China (Yunnan) were scored as Palaearctic.

Outgroup species are not scored for biogeography, as they stand as representatives of families/subfamilies with a wider distribution. For diurnality/nocturnality, outgroup taxa in Dasytidae, Malachiidae, Melyridae s.str., Mauroniscidae and Rhadalidae are coded as diurnal, as these families consist almost entirely of diurnal species. The more distant outgroup taxa Cleridae, Trogossitidae and Acanthocnemidae are not scored for this analysis.

3. Results

3.1. Phylogeny

The nine different datasets examined are indicated in parentheses {}. A tree resulting from BI of the largest dataset {3} is shown (Fig. 1). BI, ML and PA analyses showed similar topologies and levels of support for clades (see Supplementary Table S1). The length of the shortest PA tree was 3749 steps.

Eleven clades were consistently recovered in all analyses (capital letters in brackets refer to Fig. 2): 1. Prionoceridae (A). 2. *Prionocerus*, including the species *P. bicolor*, *P. coeruleipennis* and an undescribed species (D). 3. The "*Idgia flavirostris*-species group", including *I. flavirostris* and an undescribed species related to *I. granulipennis* Fairmaire, 1891 (E). 4. The "*I. oculata*-species group", including *I. oculata* and *I. maculatithorax* (F). 5. The "*I. pallidicolor*-species group", which includes *I. pallidicolor*, *I. inapicalis*, *I.* n.sp.2 and *I.* n.sp.5 (G). 6. The "*I. caeruleiventris*-species group", including *I. caeruleiventris* and *I. cyanocephala* (H). 7. A clade of *Idgia* from Sundaland, here designated as "Sundaland-1", including *I. cincta*, *I.* cf. *subcostulata* and *I.* n.sp.6 (I). 8. A clade of *Idgia*, designated as "Indochina-1", which includes *I.* n.sp.1 and *I.* n.sp.4 and an unidentified larva (J). 9. A clade of *Prionocerus* and *I. viridescens* as a sister taxon. 10. A clade comprising the "*I. caeruleiventris*-species-group" and, as its sister group, two unidentified larvae from Laos (K). 11. A clade of *P. bicolor* and *P. coeruleipennis* (M).

The deep split in Prionoceridae, roughly corresponding to Majer's (1987) Lobonychini and Prionocerini (given subfamily rank, Lobonychinae and Prionocerinae, by Bocakova et al. 2012) was observed in all trees (B and C in Fig. 2), except those obtained from datasets {4} and {8}, i.e. when only mitochondrial data were taken into account.

The following four groupings were shown consistently in BI, ML and PA analyses from datasets {1}–{3}, but not always when only one set of genes was examined ({4}–{8}): 1. A clade of *Idgia* here termed "Indochina-Indonesia-Africa", which contains *I. fulvicollis* from E Africa, three species from Indochina (*I. particularipes*, *I. varicornis* and *I.* n.sp.3), as well as an unidentified species from Sumatra (N). 2. A clade of *Idgia* here termed "Sundaland-Arabia", containing *I. setifrons*, *I.* n.sp.7, *I.* n.sp.8, *I.* n.sp.9, *I.* n.sp.10 and *I. arabica* (O). 3. A clade comprising the *I. pallidicolor*-group and the above mentioned "Indochina-1" clade as sister groups (P). 4. A clade comprising, as sister groups, the *Prionocerus* + *Idgia viridescens* lineage and the lineage containing the *I. caeruleiventris*-group and two unidentified larval samples (L).

The monophyly of *Idgia* is rejected in all analyses apart from {1}, which does not contain data for the *I. flavirostris*-group. *Prionocerus* was almost always nested as a clade within *Idgia* (in all analyses except {1} and {4}). *Idgia viridescens* was consistently shown as a sister species of *Prionocerus*, while the *I. flavirostris* species group was resolved as sister group to *Lobonyx* in all analyses containing nuclear DNA data (all except {4} and {7}).

All species represented by more than one sample were recovered as monophyla in all analyses, the only exception being *I. inapicalis*, which turned out to be paraphyletic in relation to *I. pallidicolor*.

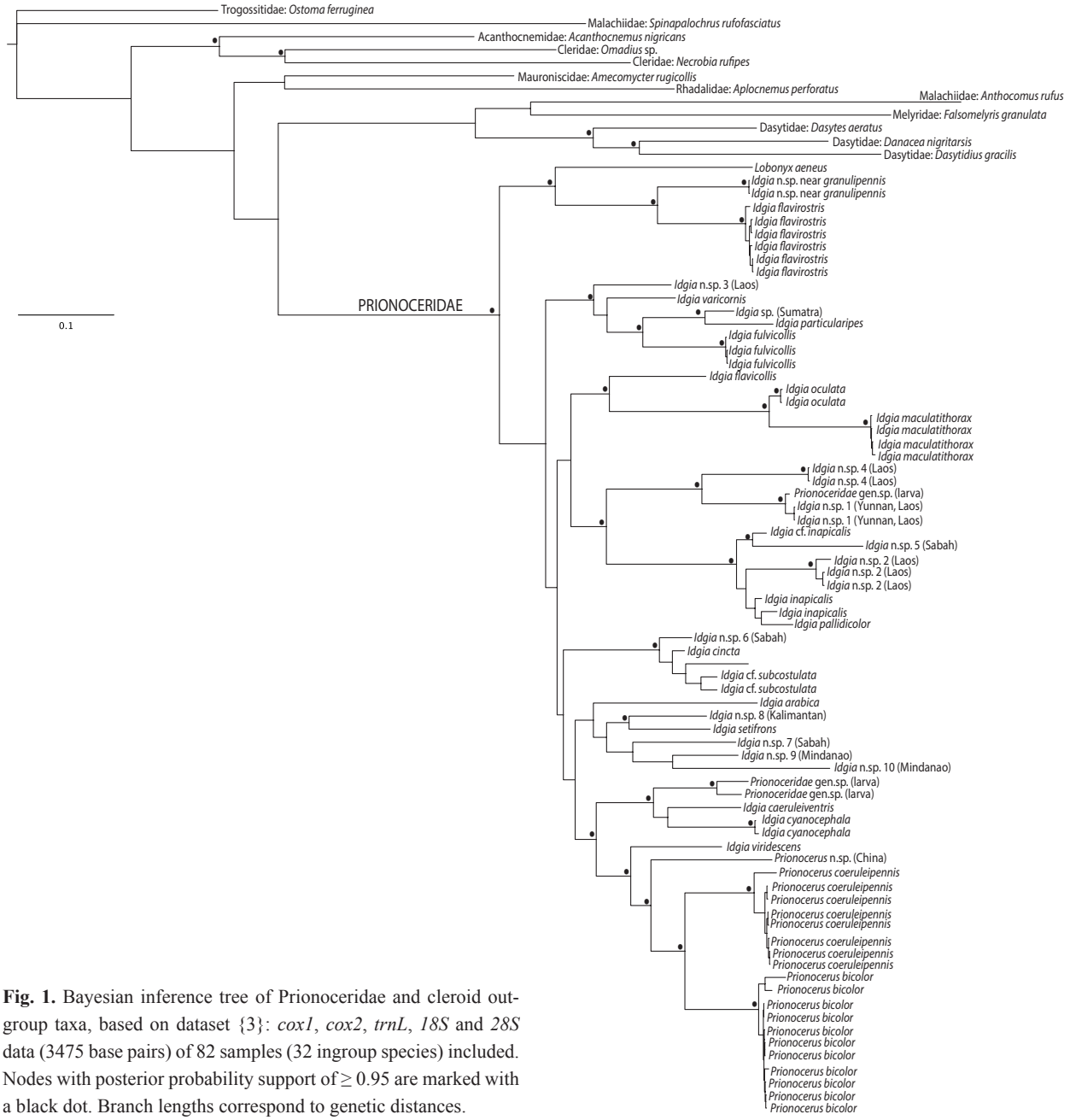

Fig. 1. Bayesian inference tree of Prionoceridae and cleroid outgroup taxa, based on dataset {3}: *cox1*, *cox2*, *trnL*, *18S* and *28S* data (3475 base pairs) of 82 samples (32 ingroup species) included. Nodes with posterior probability support of ≥ 0.95 are marked with a black dot. Branch lengths correspond to genetic distances.

3.2. Genetic distances

A complete list of the genetic similarity percentages (HKY85 model) among all samples for the *cox1* gene is given in Supplementary Table S2. A summary of genetic variation between major clades (genera and species groups), species within a group and within species is given in Table 3. We found up to 4.9% intraspecific divergence. Separate species within the same clade showed divergences between 3.7 and 13.1%. The highest genetic divergence is 16%.

3.3. Diurnality and nocturnality

BI and PA trees under the constraint of a single origin of nocturnality showed suboptimal scores compared to optimal trees, but for PA we were unable to reject the hypothesis that they were significantly suboptimal. Constraint tree 1 (assuming *Idgia fulvicollis* to be diurnal) score was 3768, and constraint 2 (assuming *I. fulvicollis* to be nocturnal) was 3760, compared to optimal tree score 3749. Both constraints were found to not be significantly different from optimal resolutions using the non-parametric Templeton Test (constraint 1: p-value 0.2287, constraint 2: 0.2859). BI analysis for constraint-1 showed poor support for all major clades within Prionoceridae, with pp-values not exceeding 0.25 (harmonic mean –19871.86

Table 3. Pairwise distances (p-distance) from *cox1* sequence data, between genera and species groups (top section), species within species groups (middle section) and individuals within species (lower section). N1 denotes the number of specimen pairs examined; N2 is the number of samples in total (first clade plus second clade).

	Mean	SD	Min.	Max.	N1	N2
Lobonyx vs *Idgia flavirostris* group	12,44	1,011	11,1	13,9	8	9
Lobonyx vs "Indochina-Indonesia-Africa clade"	13,50	0,611	12,7	14,2	7	8
Lobonyx vs *Idgia flavicollis*	12,00	0,000	12,0	12,0	1	2
Lobonyx vs *Idgia oculata* group	13,43	0,550	12,7	14,0	6	7
Lobonyx vs "Indochina-1" clade	14,44	1,299	13,3	16,0	5	6
Lobonyx vs. *Idgia pallidicolor* group	14,21	0,445	13,5	14,9	8	9
Lobonyx vs "Sundaland-1" clade	13,95	0,661	13,5	14,9	4	5
Lobonyx vs "Sundaland-Arabia" clade	13,62	0,567	13,1	14,7	6	7
Lobonyx vs *Idgia caeruleiventris* group	13,43	0,462	12,9	13,7	3	4
Lobonyx vs *Idgia viridescens*	14,30	0,000	14,3	14,3	1	2
Lobonyx vs *Prionocerus*	13,53	0,700	12,3	14,7	20	21
Idgia flavirostris group vs "Indochina-Indonesia-Africa" clade	11,43	1,178	9,4	13,6	56	15
Idgia flavirostris group vs *Idgia flavicollis*	12,34	0,571	11,6	13,6	8	9
Idgia flavirostris group vs *Idgia oculata* group	12,58	1,359	10,1	14,7	48	14
Idgia flavirostris group vs "Indochina-1" clade	12,69	0,832	11,5	14,8	40	13
Idgia flavirostris group vs *Idgia pallidicolor* group	11,61	0,877	9,9	13,6	64	16
Idgia flavirostris group vs "Sundaland-1" clade	13,05	0,768	11,8	14,4	32	12
Idgia flavirostris group vs "Sundaland-Arabia" clade	12,56	0,981016624	11,0	14,6	48	14
Idgia flavirostris group vs *Idgia caeruleiventris* group	13,95	0,948	12,1	15,9	24	11
Idgia flavirostris group vs *Idgia viridescens*	13,30	1,115	11,2	14,7	8	9
Idgia flavirostris group vs *Prionocerus*	12,80	1,189	10,2	15,5	160	28
"Indochina-Indonesia-Africa" clade vs *Idgia flavicollis*	10,33	0,522	9,4	10,9	7	8
"Indochina-Indonesia-Africa" clade vs *Idgia oculata* group	11,26	0,91276914	9,3	13,0	42	13
"Indochina-Indonesia-Africa" clade vs "Indochina-1" clade	12,71	0,477589734	11,7	13,5	35	12
"Indochina-Indonesia-Africa" clade vs *Idgia pallidicolor* group	11,78	0,946	10,0	15,1	56	15
"Indochina-Indonesia-Africa" clade vs "Sundaland-1" clade	10,52	0,495	9,5	11,5	28	11
"Indochina-Indonesia-Africa" clade vs "Sundaland-Arabia" clade	11,07	0,943	9,2	13,1	42	13
"Indochina-Indonesia-Africa" clade vs *Idgia caeruleiventris* group	12,05	0,943	10,8	14,0	21	10
"Indochina-Indonesia-Africa" clade vs *Idgia viridescens*	11,61	0,915	10,5	13,5	7	8
"Indochina-Indonesia-Africa" clade vs *Prionocerus*	10,17	1,241	8,0	13,8	140	27
Idgia flavicollis vs *Idgia oculata* group	10,85	0,267	10,5	11,3	6	7
Idgia flavicollis vs "Indochina-1" clade	12,10	0,604	11,5	12,8	5	6
Idgia flavicollis vs *Idgia pallidicolor* group	10,96	1,311	9,3	12,6	8	9
Idgia flavicollis vs "Sundaland-1" clade	11,20	0,216	10,9	11,4	4	5
Idgia flavicollis vs "Sundaland-Arabia" clade	11,82	0,214	11,6	12,2	6	7
Idgia flavicollis vs *Idgia caeruleiventris* group	12,13	0,306	11,8	12,4	3	4
Idgia flavicollis vs *Idgia viridescens*	12,30	0,000	12,3	12,3	1	2
Idgia flavicollis vs *Prionocerus*	11,06	1,046	10,0	12,7	20	21
Idgia oculata group vs "Indochina-1" clade	13,39	1,209830424	11,4	14,5	30	11
Idgia oculata group vs *Idgia pallidicolor* group	12,17	1,203318034	9,7	14,3	48	14
Idgia oculata group vs "Sundaland-1" clade	11,68	0,919002295	9,5	13,1	24	10
Idgia oculata group vs "Sundaland-Arabia" clade	12,55	1,126942767	10,2	14,3	36	12
Idgia oculata group vs *Idgia caeruleiventris* group	13,44	0,874	11,9	14,9	18	9
Idgia oculata group vs *Idgia viridescens*	14,18	0,828	12,8	14,9	6	7
Idgia oculata group vs *Prionocerus*	13,54	0,738	12,0	14,9	120	26
"Indochina-1" clade vs *Idgia pallidicolor* group	12,08	0,822363698	10,6	14,3	40	13
"Indochina-1" clade vs "Sundaland-1" clade	13,06	0,717800001	12,0	14,5	20	9
"Indochina-1" clade vs "Sundaland-Arabia" clade	12,48	0,917298633	10,8	14,4	30	11
"Indochina-1" clade vs *Idgia caeruleiventris* group	12,59	0,596	11,2	13,5	15	8
"Indochina-1" clade vs *Idgia viridescens*	12,92	0,249	12,6	13,3	5	6
"Indochina-1" clade vs *Prionocerus*	12,74	0,460	11,8	13,6	100	25
Idgia pallidicolor group vs "Sundaland-1" clade	12,38	0,852	10,9	13,7	32	12
Idgia pallidicolor group vs "Sundaland-Arabia" clade	12,84	0,815	11,2	14,5	48	14
Idgia pallidicolor group vs *Idgia caeruleiventris* group	13,24	1,098	11,1	14,9	24	11
Idgia pallidicolor group vs *Idgia viridescens*	13,73	0,740	12,9	15,3	8	9
Idgia pallidicolor group vs *Prionocerus*	12,24	0,668	10,8	14,5	160	28
"Sundaland-1" clade vs "Sundaland-Arabia" clade	12,09	0,883135061	10,6	13,5	24	10
"Sundaland-1" clade vs *Idgia caeruleiventris* group	12,34	0,516	11,4	13,2	12	7

Table 3 continued.

	Mean	SD	Min.	Max.	N1	N2
"Sundaland-1" clade vs *Idgia viridescens*	12,85	0,493	12,3	13,4	4	5
"Sundaland-1" clade vs *Prionocerus*	11,41	0,819	10,1	13,6	80	24
"Sundaland-Arabia" clade vs *Idgia caeruleiventris* group	11,92	0,736	10,9	13,7	18	9
"Sundaland-Arabia" clade vs *Idgia viridescens*	12,82	0,768	12,0	14,1	6	7
"Sundaland-Arabia" clade vs *Prionocerus*	12,06	0,835	10,2	13,7	120	26
Idgia caeruleiventris group vs *Idgia viridescens*	12,77	0,289	12,6	13,1	3	4
Idgia caeruleiventris group vs *Prionocerus*	11,98	0,760	10,5	13,4	60	23
Idgia viridescens vs *Prionocerus*	10,83	0,601	9,8	13,0	20	21
Idgia caeruleiventris group	10,10	0,780	9,5	10,6	2	3
Idgia flavirostris group	9,42	0,444835686	8,8	10,3	12	8
Idgia oculata group	4,76	0,311390889	4,3	5,3	8	6
Idgia pallidicolor group	7,96	2,5614179	3,7	10,0	24	8
"Indochina-1" clade	10,50	0,352	9,9	10,9	6	5
"Indochina-Indonesia-Africa" clade	8,52	0,784	6,2	10,1	18	7
"Sundaland-1" clade	6,16	0,921	5,0	7,4	5	4
"Sundaland-Arabia" clade	10,99	1,115	9,2	13,1	15	6
Prionocerus n.sp. vs *Prionocerus coeruleipennis/bicolor*	10,94	0,444	9,8	11,4	19	20
Prionocerus coeruleipennis vs *Prionocerus bicolor*	8,41	0,420	7,6	9,4	88	19
Idgia cf. *subcostulata*	3,00	0,000	3,0	3,0	1	2
Idgia cyanocephala	1,70	0,000	1,7	1,7	1	2
Idgia flavirostris	0,97	0,489	0,2	1,7	15	6
Idgia fulvicollis	0,33	0,115	0,2	0,4	3	3
Idgia inapicalis	2,90	0,000	2,9	2,9	1	2
Idgia maculatithorax	0,33	0,320	0,0	0,8	6	4
Idgia oculata	0,60	0,000	0,6	0,6	1	2
Idgia n.sp. near *granulipennis*	0,20	0,000	0,2	0,2	1	2
Idgia n.sp.1	1,47	1,100	0,2	2,1	3	3
Idgia n.sp.2	2,33	1,343	0,8	3,3	3	3
Idgia n.sp.4	0,80	0,000	0,8	0,8	1	2
Prionocerus bicolor	1,25	1,158	0,0	3,5	55	11
Prionocerus coeruleipennis	2,00	1,650	0,1	4,9	28	8

compared to optimal tree: –19803.58). For contraint-2, however, the phylogeny was much better supported, with only slightly lower pp-values than in the optimal tree (–19843.89). Bayes factor scores indicated that constraint-1 and constraint-2 were not significantly worse, in accordance with the non-parametric tests in PA analyses.

Our ancestral reconstruction of diurnality and nocturnality (Fig. 3) shows, based on our sampling, that there was a single evolutionary event for nocturnality within the melyrid clade. Diurnality, on the other hand, evolved multiple times within Prionocerinae. The precise number of diurnality events depends on coding schemes employed (Table 4).

4. Discussion

4.1. Phylogenetic relationships and classification

The systematics of the 158 described species of prionocerid beetles is very poorly known with only few recent studies dedicated to their taxonomy (CONSTANTIN 2009; GEISER 2010). Our study provides the first test of various morphological hypotheses of the group, since the last partial revision nearly 100 years ago (CHAMPION 1919) and the subsequent inclusion of *Lobonyx* within the family (CROWSON 1964). Currently, taxa are assigned to two subfamilies (Lobonychinae and Prionocerinae) in the family Prionoceridae (MAJER 1987; BOCAKOVA et al. 2012). Within these subfamilies one genus is recognised in Lobonychinae (*Lobonyx*) and two in Prionocerinae (*Idgia* and *Prionocerus*). Our analyses provide robust support for the deep split between Lobonychinae and Prionocerinae (see Figs. 1 and 2), supporting the morphological delineation first outlined by MAJER (1987). However, several species currently placed in *Idgia* (*flavirostris* species group), not studied by MAJER, group with the Lobonychinae clade and we suggest their placement in this subfamily. A description of a new genus will be necessary, given their molecular and morphological distinctiveness from *Lobonyx* (currently in progress; M. Geiser, unpublished).

Currently, Lobonychinae seems to be mainly defined on the basis of symplesiomorphies, which include claws with membraneous lobe, head with sharply marked fron-

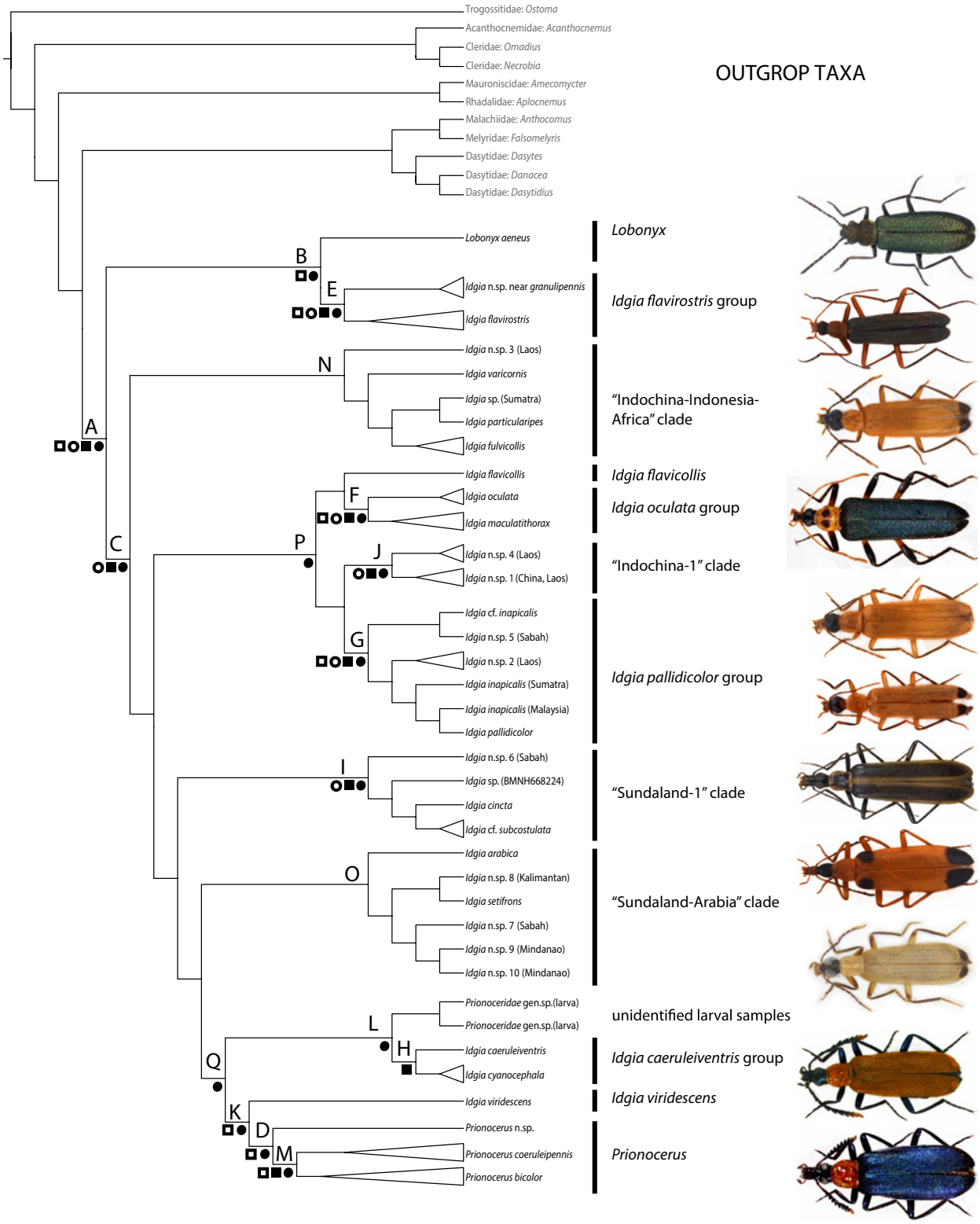

Fig. 2. Bayesian inference tree (condensed from Fig. 1) showing relationships of species, species groups and genera. Clades with good support in either BI, ML or PA analyses are indicated with letters A–Q. Supporting posterior probability pp and bootstrap values for these clades are shown in Supplementary Table S1. Full circles: Nodes supported in BI with pp-values > 0.95. Full squares: Nodes supported in ML with bootstrap values > 90. Empty circles: Nodes supported in PA with bootstrap values > 90. Empty squares: Nodes with additional morphological support. Typical representative of each clade are figured. From top to bottom: *Lobonyx aeneus*, *Idgia flavirostris*, *Idgia varicornis*, *Idgia oculata*, *Idgia* n.sp.2, *Idgia pallidicolor*, *Idgia cincta*, *Idgia* sp. neare *arabica*, *Idgia setifrons*, *Prionocerus* n.sp., *Prionocerus coeruleipennis* (not to scale).

toclypeal suture and the structure of the endophallic sclerites, which were briefly described and figured for *Lobonyx* by Constantin (2009).

The Prionocerinae are well supported based on both molecular data and morphology (Majer 1987). Morphological synapomorphies of Prionocerinae include simple claws, frons and clypeus separated by a transverse furrow, without sharply marked suture, and endophallus with a pair of basal sclerites and two rows of denticles, which extend up to the ostium, without ostial lamellae (as shown in Majer 1987: fig. 285).

The genus *Prionocerus* contains eight nominate species (Geiser 2010). The monophyly of *Prionocerus* was supported in our analyses, which included three species (Fig. 1). Geiser (2010) discussed four taxa as being problematic to place within or outside *Prionocerus*, based on antennal morphology and other characters. Among these, *P. wittmeri* Geiser, 2010, *Idgia triserrata* Champion, 1919 and *I. belli* Gorham, 1895 were unavailable for the present study, while *Idgia viridescens* was herein strongly supported as sister group to *Prionocerus* (Fig. 1) and may need to be moved formally into this genus. Supporting this arrangement is the morphological similarity of the antennae, although in *I. viridescens* they are not as strongly flattened and serrate as in *Prionocerus*. On the other hand, antennomere shape varies between closely related species in Prionoceridae and strongly flattened antennae with triangular segments may have evolved more than once within the family, which makes it problematic to use this as sole diagnostic character of this genus (Geiser 2010). Additional molecular and morphological data are needed, before a formal re-definition of *Prionocerus* can be attempted.

The genus *Idgia* currently contains 139 nominate species (Pic 1921, 1926, 1927, 1931, 1934, 1941, 1942a,b, 1943a,b; Mayor 2007; Geiser 2009, 2010). Our analyses recovered *Idgia* as a paraphyletic grade, consisting of at least 7 smaller clades, with the *I. flavirostris*-species group appearing as sister group to *Lobonyx* (see above; Fig. 1), *Prionocerus* plus *I. viridescens* represents a terminal clade. No morphological synapomorphies support *Idgia* as a monophylum (Majer 1987; own data).

However, the basal splits within Prionocerinae (e.g. groupings among *Idgia* and *Prionocerus*) received relatively weak support within our analyses, with short branch lengths. This might be indicative of patterns of rapid evolution at a species-group/genus level or might simply reflect a lack of appropriate genetic markers. Increased taxon sampling and appropriate markers will be required to investigate this further.

Critical to understanding the content of the genus *Idgia* is resolving the position of the type species (*I. terminata*) and how other species group in relation to this species and *Prionocerus*. Unfortunately, *I. terminata* is not sampled, but we sampled the morphologically similar species *I. fulvicollis* from the same geographic area. *I. fulvicollis*, and by inference *I. terminata*, are shown to be members of the "Indochina-Indonesia-Africa" clade in our analysis (see Results chapter). This grouping, however, is only supported by molecular data so far. There is a similar situation for the type species of the junior synonym *Deromma*, *D. melanura* Kollar & Redtenbacher, 1844, which is morphologically most similar to *I. particularipes*. It may therefore also be included in the "Indochina-Indonesia-Africa" clade. Following morphological study of nearly all described taxa of *Idgia* (M. Geiser, unpublished data), a number of potentially monophyletic species groups was recognised within *Idgia*, which may deserve genus or subgenus status, depending on the available data and their phylogenetic position in relation to the type species of *Idgia* and *Prionocerus* (see Fig. 2).

Two species groups, *Idgia oculata* and *Idgia pallidicolor*, were well supported by molecular analyses (Fig. 2). The species group of *Idgia oculata* consists of *I. oculata* and *I. maculatithorax*. These species show a number of morphological peculiarities: the absence of male protarsal combs, which is one of the main diagnostic characters of Prionoceridae; the short, barrel-shaped coxital styli of the ovipositor and the sexually dimorphic, peculiarly formed 11th antennomere. The *Idgia oculata*-group may well deserve to be established as a different genus in the future. *I. flavicollis* is suggested as its sister group in the present molecular tree, for which no morphological support was found.

The *I. pallidicolor* species group was treated as a single species by Champion (1919). It includes, however, a number of morphologically distinct species, clearly separable by the shape of their male genitalia, size and colour pattern. These are *I. inapicalis*, *I. coomani* Pic, 1931, *I. dohertyi* Pic, 1912, *I. maculicornis* Pic, 1925 and a number of undescribed species. Their main synapomorphy is the peculiar shape of the 6th ventrite in males, which has a pair of deep incisions at the apical margin. The *pallidicolor* species group is shown to be monophyletic in the present phylogeny. A clade of pale coloured *Idgia*, mainly from Laos ("Indochina-1") was a sister to this clade. Morphological support for the "Indochina-1" clade and its relationship to the *pallidicolor*-group is lacking.

The genus *Lobonyx* currently comprises 11 species (Mayor 2007; Constantin 2009). *Eulobonyx* Kraatz, 1882 was placed as a junior subjective synonym (Pic 1937; Constantin 2009). As only one species was available for the present study, the monophyly of the genus could not be tested. However, its position as sister group to a clade including *Prionocerus* and *Idgia* supports Majer's (1987) and Bocakova et al.'s (2012) findings.

4.2. Genetic divergence and species identification

Genetic divergence within beetle families is relatively poorly understood, and only a few papers provide quantitative data on genetic variation within and between species of a clade (e.g. Meier et al. 2008; Hendrich et al. 2010; Riedel et al. 2010). Our study has shown that

there is little overlap in genetic variation between the infra- and interspecific levels (see Table 3). This suggests a match to some extent between traditional and molecular taxonomy. Inter- and intraspecific *cox1* variation within Prionoceridae is comparable to observed variation in Australian Dytiscidae (Hendrich et al. 2010) but not as observed in tropical weevils (Riedel et al. 2010). For example, the smallest observed interspecific divergence was 16.5% in a genus *Trigonopterus* (Riedel et al. 2010) substantially above the minimum recorded in this study (3.7%).

Generally observed morphological species boundaries were all congruent with clades in our analysis, with one possible exception in *Idgia inapicalis*. The two samples of *I. inapicalis* included in our analyses were placed into the same clade with its close relative *I. pallidicolor*, suggesting they are close relatives or potentially the same taxon (*cox1* divergence 3.7–4.7%). It is likely these two species are separate given they show morphological differences in the structure of the male genitalia. Further taxonomic work and a broader geographical sampling will be required to investigate molecular and morphological variation in *I. inapicalis* and *I. pallidicolor*. Our study provided interesting results for *Idgia* n.sp.1 ("Indochina-1 clade"). It was possible to assign the female from Laos to the male from South China based on molecular data, which would have been difficult to achieve by morphology – given male genitalia is an important diagnostic tool. Also, a larval specimen from Central Laos was shown to likely belong to the same species (*cox1* divergence 2.1%). Other larval specimens collected in Laos were shown to be closely related (*cox1* divergence 5.2%) and may belong to a single species, but unfortunately could not be associated with any of the species represented by adults in our study. Using mitochondrial DNA sequences ("Barcoding") to facilitate identification of holometabolous insect larvae is a relatively new technique, already successfully applied in a number of beetle families, e.g. Dytiscidae (Miller et al. 2005), Elmidae (Curiel & Morrone 2012), Cerambycidae (Lim et al. 2013) and Chrysomelidae (García-Robledo et al. 2013). Overall, our data provide a strong foundation to assign prionocerid specimens to subfamilies and genera, and in some cases to species.

Table 4. List of Prionoceridae species examined for life history strategy. Species are categorised based on field observations, specimen label data and adult morphology (size of eyes and bright metallic vs. dark or testaceous body colour). The source of information allowing each species to be categorised is given.

diurnal	**source of information**
Idgia flavicollis	Aston 2011
Idgia flavirostris	Aston 2011
Idgia fulvicollis (?)	label data; L. Bocak pers. comm.
Idgia maculatithorax	own observations
Idgia n.sp. near *granulipennis*	own observations
Idgia oculata	Aston 2011
Lobonyx aeneus	Bahillo & López Colón 2003
Prionocerus bicolor	own observations
Prionocerus coeruleipennis	own observations
Prionocerus n.sp.	label data
nocturnal	**source of information**
Idgia arabica	label data
Idgia caeruleiventris	label data
Idgia cf. *inapicalis*	label data
Idgia cf. *subcostulata*	label data
Idgia cincta	label data
Idgia cyanocephala	label data
Idgia inapicalis	label data
Idgia n.sp.1 (China, Laos)	own observations
Idgia n.sp.2 (Laos)	own observations
Idgia n.sp.3 (Laos)	own observations
Idgia n.sp.4 (Laos)	own observations
Idgia n.sp.5 (Sabah)	own observations
Idgia n.sp.6 (Sabah)	own observations
Idgia n.sp.7 (Sabah)	own observations
Idgia n.sp.8 (Kalimantan)	morphology
Idgia n.sp.9 (Mindanao)	label data
Idgia n.sp.10 (Mindanao)	label data
Idgia pallidicolor	label data
Idgia particularipes	own observations
Idgia setifrons	own observations
Idgia sp. Sumatra	label data
Idgia sp. BMNH668224	inferred from related species
Idgia varicornis	own observations
Idgia viridescens	label data

4.3. Diurnality vs. nocturnality

Nocturnality appears to be a relatively common life history strategy in beetles, and evolutionary transition between diurnality and nocturnality seems to be frequent. However, the presence of nocturnality in many prionocerids is an exceptional trait within the predominantly diurnal melyrid lineage. Only a small number of species in the melyrid lineage, mostly Malachiidae, were reportedly found at light traps or collected by sampling during night-time (label data of museum specimens and own observations). It is therefore interesting to understand how many transitions between nocturnality and diurnality have occurred in Prionoceridae and what are the possible causal factors.

The ancestral state reconstruction (Fig. 3) suggests the common ancestor of Prionoceridae to be likely a diurnal species. All species of the clade including *Lobonyx* and the *Idgia flavirostris* group are assumed to be diurnal. The ancestral state for Prionocerinae, however, was very probably nocturnal with this evolutionary event being an important step towards the presence of nocturnality in a majority of Prionocerinae species. Furthermore, at least two evolutionary transitions from nocturnality back to diurnal life style occurred within Prionocerinae. These clades are *Prionocerus*, the *Idgia oculata*-species group plus *I. flavicollis* and probably the African clade of *Idgia*, including *I. fulvicollis*. Although we cannot re-

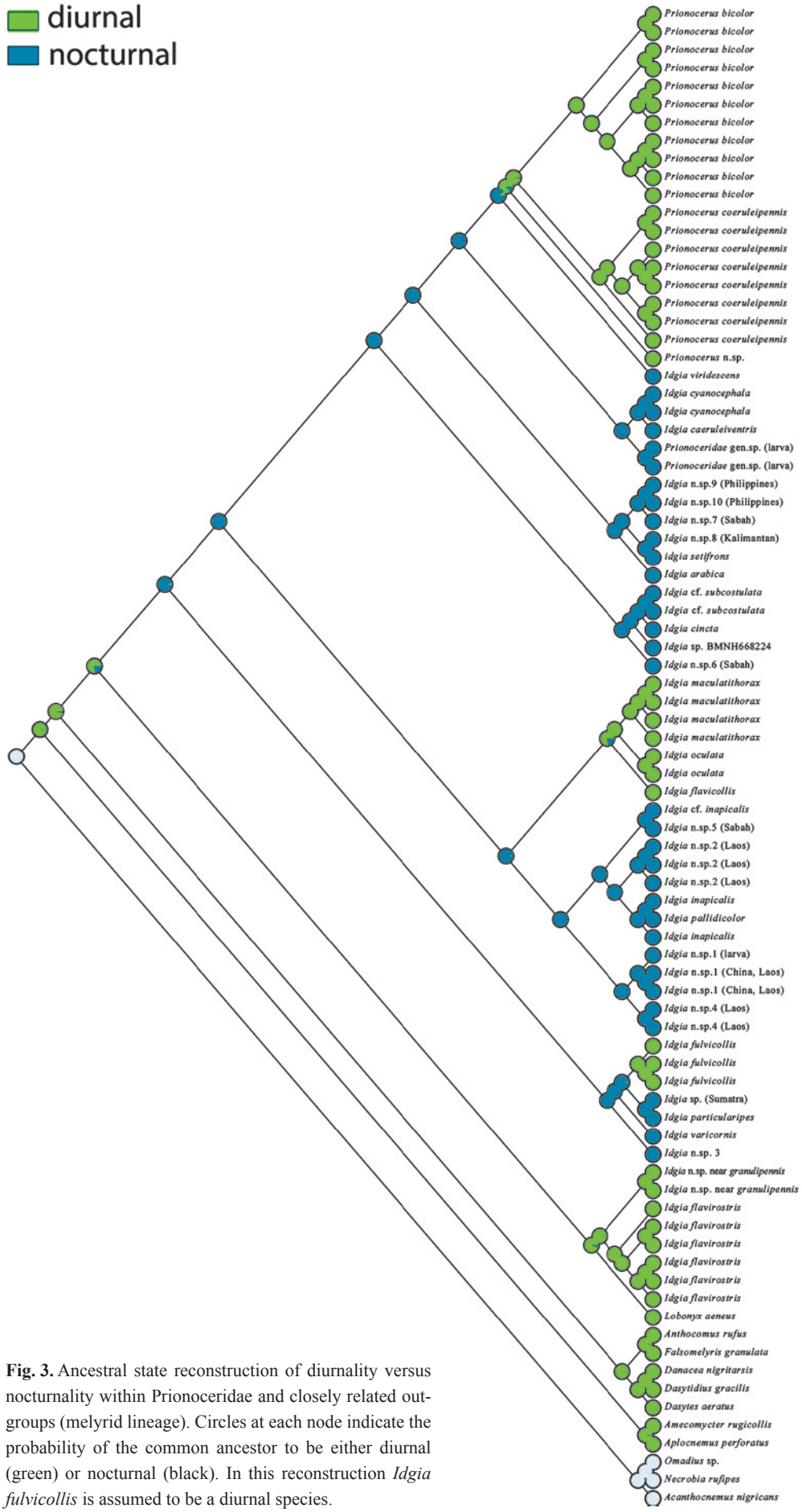

Fig. 3. Ancestral state reconstruction of diurnality versus nocturnality within Prionoceridae and closely related outgroups (melyrid lineage). Circles at each node indicate the probability of the common ancestor to be either diurnal (green) or nocturnal (black). In this reconstruction *Idgia fulvicollis* is assumed to be a diurnal species.

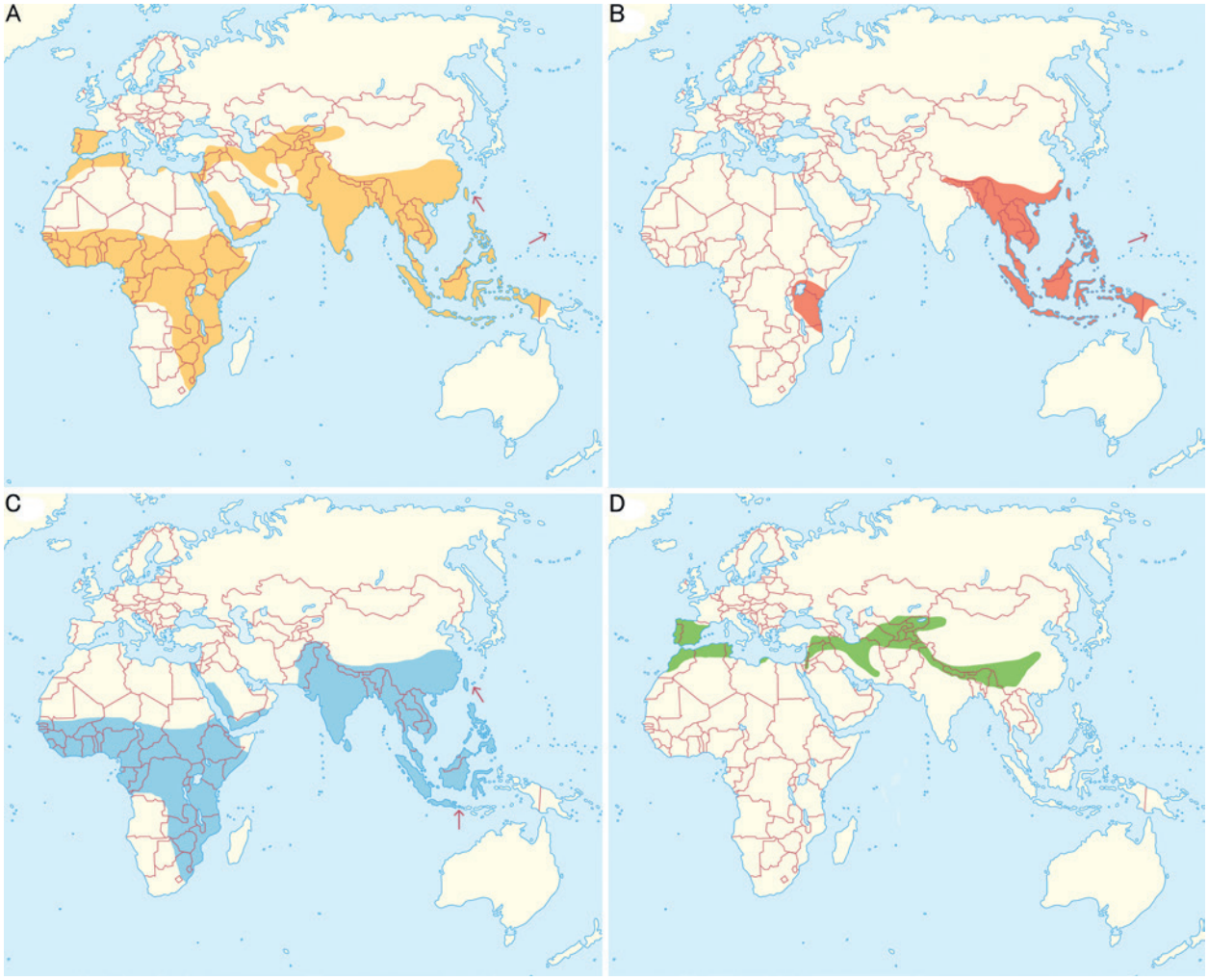

Fig. 4. Contemporary distribution of Prionoceridae (A) and the three described genera: *Prionocerus* (B), *Idgia* (C) and *Lobonyx* (D). Dubious records are omitted. Prionoceridae are limited to the Old World.

ject the hypothesis that either nocturnal or diurnal species are monophyletic (both BI and PA topology tests were not significant) – suggesting a single evolutionary transition – and unconstrained ancestral state reconstructions based on optimal trees suggest multiple transitions. Multiple changes back to diurnality may reflect an evolutionary advantage of diurnal habits for at least some species, possibly associated with flower/pollen feeding behaviour. Very large eyes, as a trait associated with nocturnality, are still present in at least some diurnal species (genus *Prionocerus*). Further research is required to understand the causal factors for the multiple transitions in prionocerids.

4.4. Biogeography

Extant members of Prionoceridae are distributed in the Oriental, Afrotropical and Palaearctic biogeographic regions, with two species extending to the Australian Region (New Guinea) (Fig. 4), being absent from Madagascar, Australia and the whole Western Hemisphere. A recently described Eocene prionocerid larva from Canada (Lawrence et al. 2008) suggests that they were more widely distributed in the past. One species of Oriental origin, *Prionocerus coeruleipennis*, even extends to parts of Melanesia and Micronesia in the Pacific (Wittmer 1958; Geiser 2010). Within the Palaearctic, prionocerids are limited to areas of warmer climate: The Mediterranean basin, the Near East, the Arabian Peninsula, Central Asia, the Himalayas, South and Central China and the southernmost islands of Japan (Yaeyama Is.). Within the Afrotropics, they extend to most regions, except the Southwest (Angola, Namibia, western South Africa), but are not rich in species. In summary, prionocerids are most widespread and species-rich within the Oriental (Indo-Malayan) region, which is suggestive of their origin in this region. Our tree provides the first opportunity to investigate such biogeographic patterns from a historical perspective.

Our ancestral state reconstruction of the geographic area of origin based on the BI tree is shown in Fig. 5. The analysis suggests Indochina as the most likely region of origin of Prionoceridae. Both in terms of numbers of species and major lineages, this is one of the most diverse

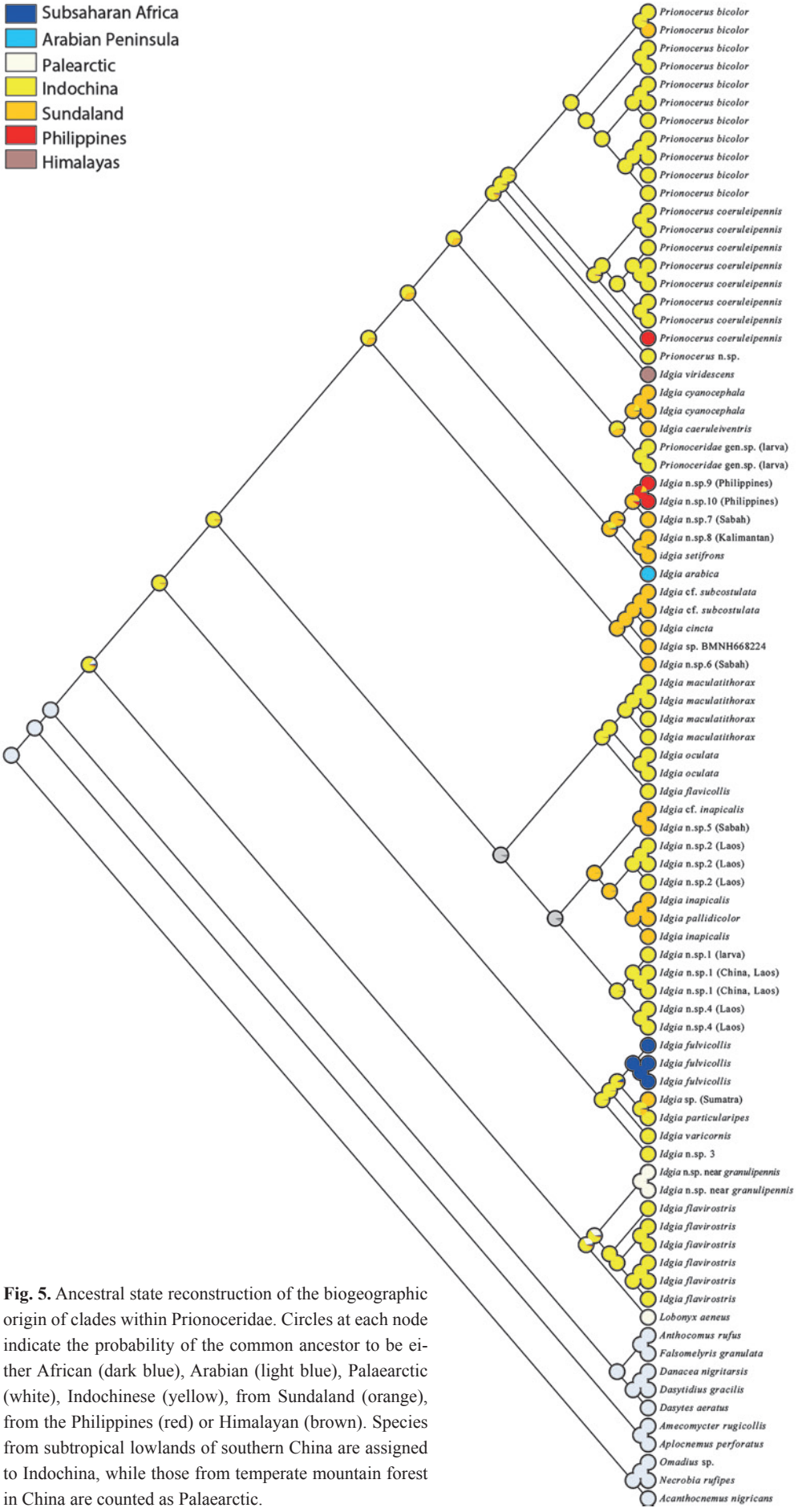

Fig. 5. Ancestral state reconstruction of the biogeographic origin of clades within Prionoceridae. Circles at each node indicate the probability of the common ancestor to be either African (dark blue), Arabian (light blue), Palaearctic (white), Indochinese (yellow), from Sundaland (orange), from the Philippines (red) or Himalayan (brown). Species from subtropical lowlands of southern China are assigned to Indochina, while those from temperate mountain forest in China are counted as Palaearctic.

areas (based on observed museum specimens – M. Geiser, unpublished data). However, this result may be due to taxon sampling, which in our study is strongly biased towards some geographic areas (in particular Laos). Species from other species-rich areas, e.g. India, are poorly represented. In some common and widespread species (e.g. *Prionocerus coeruleipennis*), the sampling is also biased towards Indochinese specimens, which may not always reflect their true area of origin. A wider sampling of taxa and geographic localities within species will be necessary to provide a critical test to our hypotheses.

Among the two major lineages of Prionoceridae, Lobonychinae are most diverse along the East Palaearctic-Oriental faunal border, particularly in the Himalayas and southern China (Constantin 2009; M. Geiser, unpublished data). A more comprehensive species sampling within *Lobonyx* would be necessary to draw conclusions about the relationships of western (e.g. *Lobonyx aeneus*) and eastern Palaearctic species, in order to determine their likely area of origin. Prionocerinae, on the other hand, is mainly a tropical group, showing three distinct centers of species diversity in the following areas: The Western Ghat mountain system in South India, the Indochinese Peninsula and Sundaland (Champion 1919; M. Geiser, unpublished data). China also has a relatively rich fauna, but with many species restricted to the southernmost parts, adjacent to Laos and Vietnam (Yang et al. 2012). The present analyses suggest a relatively recent dispersal of Prionoceridae to both Sub-Saharan Africa and the Arabian Peninsula, achieved independently by at least two lineages ("Indochina-Indonesia-Africa" and "Sundaland-Arabia"), both originating in the Oriental region. Morphological studies (M. Geiser, unpublished data) suggest a monophyletic origin of the prionocerid fauna in Subsaharan Africa, with the exception of *Idgia apicalis* (Gerstaecker, 1871) and *Prionocerus coeruleipennis*, the latter being probably an anthropogenic introduction (Champion 1919; Geiser 2010). The present study highlights not only a large diversity of species, but also of major lineages, within two global hotspots: Indo-Burma and Sundaland (Myers et al. 2000).

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Electronic Supplement Files

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File 1: geiser&al-prionoceridaephylogeny-asp2015-electronicsupplement-1.xlsx **— Table S1.** List of Prionoceridae clades as shown in Fig. 2. Posterior probability (pp) values obtained from Bayesian inference (BI) and bootstrap values obtained from Maximum likelihood (ML) and Parsimony analyses are shown. Datasets used for each analyses (see Material and Methods) are given in parentheses {}. Clades, for which additional morphological support was found, are indicated (see discussion for details). Some datasets did not include enough taxa to give any information about certain clades, these are shown as "N/A". Clades indicated as "not supported" were not found in the optimal tree.

File 2: geiser&al-prionoceridaephylogeny-asp2015-electronicsupplement-2.xlsx **— Table S2.** *cox1* sequence divergence percentages found between samples. Values were calculated using the HKY85 model of sequence evolution.