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Phylogenetics of scutigeromorph centipedes (Myriapoda: Chilopoda) with implications for species delimitation and historical biogeography of the Australian and New Caledonian faunas

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Abstract

Phylogeny of the centipede order Scutigeromorpha has received recent attention from combined analyses of molecular and morphological data. Denser generic sampling, an additional marker (12S rRNA), and multiple specimens for selected species are used to explore phylogeny, biogeography and taxonomy of this charismatic group of centipedes. Among 55 specimens/27 species analysed for six genes are the first molecular data for the genera *Dendrothereua*, *Pilbarascutigera*, and *Tachythereua*, and previously unsampled species of Scutigerinae from Madagascar. Sampling density is especially increased for Thereuoneminae from Australia and New Caledonia. At the base of Scutigeromorpha, the split of Pselliodidae from Scutigerinidae + Scutigeridae is favoured by the optimal parameter set in combined analyses, but most suboptimal parameter sets instead unite pselliodids and scutigerinids. *Dendrothereua* is re-established for a Neotropical clade that variably resolves as sister to *Tachythereua* or separate from Scutigerinae, grouped with Pselliodidae and Scutigerinidae. As traditionally diagnosed, the genera that comprise most of Australian and New Caledonian diversity, *Allothereua* and *Parascutigera*, are mutually polyphyletic, though they unite as a well supported clade, sister to or including the Western Australian *Pilbarascutigera*. The main biogeographical signal within the *Allothereua/Parascutigera* clade is Western Australia as sister area to eastern Australia/New Caledonia, within which New Caledonian "*Parascutigera*" has a single origin under optimal parameter sets. Genetic variation within scutigeromorph species is appraised using samples of *Scutigera coleoptrata* throughout its native distribution plus presumed synanthropic records, and from the *Allothereua/Parascutigera* clade. Variation between six alleged narrow-range endemic species of *Parascutigera* in north Queensland is consistent with a single species.

Global diversity of scutigeromorph centipedes stands at some 200 described species, of which just under half are currently considered valid (Stoev and Geoffroy, 2004; Minelli, 2006). The classification of Scutigeromorpha was largely developed in the early 20th century by K. W. Verhoeff, who presented the first explicit phylogenetic tree of the group (Verhoeff, 1905). The current, long-standing classification recognizes three families, Scutigerinidae, Pselliodidae, and Scutigeridae, the latter divided into the subfamilies Scutigerinae and Thereuopodinae. The traditional scope of these groupings has been supported by recent analyses using combined morphological and molecular data (Edgecombe and Giribet, 2006). Scutigerinidae is composed of two genera in southern Africa and Madagascar, Pselliodidae consists of a single genus (*fide* Würmli, 2005) in the Neotropics and tropical Africa, whereas Scutigeridae embraces diversity from temperate and tropical regions around the World, with *Scutigera coleoptrata* extending the range to colder regions as a result of its synanthropic distribution. Although the status of the families was clear-cut in the study of Edgecombe and Giribet (2006), the sampled diversity of Scutigerinae was restricted to

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S. coleoptrata. Furthermore, the relationships between the three families were more problematic. Morphological data favoured Scutigerinidae as sister to Pselliodidae + Scutigeridae, whereas the inclusion of molecular data supported a sister-group relationship either between Scutigerinidae + Pselliodidae or between Scutigerinidae + Scutigeridae, depending on the analytical parameter set employed. The Neotropical genus *Dendrothereua*, traditionally identified as a single widespread species, *Scutigera linceci* (Wood, 1867), presents a biogeographical enigma in the context of the distribution of Scutigeridae. The group Scutigerinae is not otherwise represented by native species in North, Central, or northern South America (again with the exception of *S. coleoptrata*). The taxonomic status of the Neotropical lineage, as well as its relevance to the ongoing controversy over the interrelationships of scutigeromorph families, is explored here based on combined morphological and molecular data.

The 25 named scutigeromorph species or subspecies from Australia and five from New Caledonia make up about one-third of described global diversity for Scutigeromorpha as a whole. All but eight of the available specific names for Australian scutigeromorphs were published by Verhoeff (1925) in a study based on material collected in Queensland and Western Australia between 1910 and 1913. The paucity of modern studies on Australian scutigeromorphs has meant that Verhoeff's species have been tentatively accepted as valid in current catalogues of the order Scutigeromorpha (Minelli, 2006). Of the 17 species-group taxa named by Verhoeff (1925), the most prolific diversification was recognized within the genus *Parascutigera* Verhoeff, 1904, in north Queensland. Six species of this genus were named from a few sites on the Atherton Tableland in the Wet Tropics region. It is atypical for scutigeromorphs to exhibit the kind of species richness and sympatry of closely allied species that is implied by Verhoeff's taxonomy of Queensland *Parascutigera*. In other cases where Verhoeff recognized numerous congeneric species over a relatively restricted geographical extent (e.g. *Thereuopoda* in the Malay Peninsula) (Verhoeff, 1937), subsequent revision has led to extensive synonymy (Würmli, 1979). Intriguingly, however, exceptions to the general pattern of few closely related sympatric species are known. New Caledonia harbours at least four valid species of *Parascutigera* (Ribaut, 1923) that are readily distinguished morphologically (Ribaut, 1923; Würmli, 1974a) and occur in sympatry over much of their distributions on Grande Terre.

In this paper, the status of Verhoeff's species of *Parascutigera* from Queensland is reassessed as one of a few case studies in molecular variation in morphologically delimited species. Specimens of *S. coleoptrata*, regarded as a native species throughout the Mediterranean (Würmli, 1977), are sampled across the presumed native and introduced parts of its range to explore genetic variability in what taxonomists regard as an acceptable species. Molecular data offer an important source of information for addressing questions of morphological variability that plague the taxonomy of these centipedes, in which species have generally been based on few specimens, and species concepts have oscillated between narrowly diagnosed taxa with limited geographical ranges and much more variable taxa that span broad expanses of the globe.

Methods

Specimens cited herein are housed in the following institutions: Australian Museum, Sydney (AM KS); Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ DNA); The Natural History Museum, London (BMNH); Naturhistoriska riksmuseet, Stockholm (SMNH); Queensland Museum, Brisbane (QM S). Descriptive terminology generally follows recommendations by Würmli (1974b). Terminology for peristomatic structures (epipharynx and hypopharynx) is as used by Koch and Edgecombe (2006). Tergal plates are abbreviated T1–T8 (Negrea, 2003).

Taxon and gene sampling

Initial studies on phylogenetics of Scutigeromorpha using five of the markers sequenced herein sampled 19 specimens representing 14 species (Edgecombe and Giribet, 2006). Presently we supplement these data with 36 additional specimens that include 12–13 additional species, and also add sequences for an additional marker, 12S rRNA, which is more variable than the other ribosomal rRNA genes and should therefore inform upon intraspecific variability. The complete molecular character set consists of up to *ca.* 6000 bp. Details on the taxa and markers sequenced are shown in Table 1. Appendix 1 includes taxonomic authorships and vouchers for newly added specimens. Morphological characters are documented by Edgecombe and Giribet (2006) and Edgecombe and Barrow (2007), modified for the current taxon sampling as in Appendix 2, with codings for species-level terminals in Table 2.

Sampling is especially expanded within *Parascutigera* and *Allothereua* Verhoeff, 1905, genera that formed a more inclusive clade in previous studies. The sampling for *Parascutigera* in New Caledonia is expanded to include additional specimens of *P. festiva* Ribaut, 1923, and *P. latericia* Ribaut, 1923, from widely separated parts of their geographical ranges, and the first molecular data for *P. nubila* Ribaut, 1923. To sample *Parascutigera* from the south-west of Western Australia, we include data for a species that is tentatively determined as *P. sphinx* Verhoeff, 1925; the population

Table 1
List of taxa, MCZ accession numbers, localities, and GenBank accession numbers for each locus sequenced

			18S rRNA	28S rRNA	16S rRNA	COI	H3	12S rRNA
Proteroiulus fuscus	DNA100171		AF173236	AF370804	AF370866	AF370842	–	–
Lithobius variegatus rubriceps			AF000773	AF000780	AY084071	AF334311	–	–
Paralamyctes validus	DNA100297		AF334289	AF173278	AF334358	AF334330	DQ222180	–
Anopsobius neozelanicus	DNA101035		AF173248	DQ222132	AF334337	DQ222165	DQ222179	–
Craterostigmus tasmanianus	DNA100280		AF000774	DQ222133	AF370860	AF370835	AF110850*	–
Scolopendra viridis	DNA100675		DQ201419	DQ222134	DQ201425	DQ201431	DQ222181	–
Scutigerinidae								
Scutigerina malagassa	DNA101591	Madagascar	DQ222119	DQ222136	DQ222152	DQ222167	DQ222183	FJ660869
Scutigerina weberi	DNA100455	Swaziland	AY288689	AY288705/ DQ222135	AY288717	AY288741	AY428835	–
Scutigerina cf. *weberi*	DNA101590	Madagascar	DQ222118		DQ222151	DQ222166	DQ222182	FJ660870
Madagassophora hova	DNA101592	Madagascar	DQ222120	DQ222137	DQ222153	–	DQ222184	–
Pselliodidae								
Sphendononema guildingii	DNA101161	Brazil	DQ222121	DQ222138	–	–	DQ222185	–
Sphendononema guildingii	DNA101630	Brazil	DQ222122	DQ222139	DQ222154	DQ222168	DQ222186	FJ660871
Scutigeridae, Scutigerinae								
Dendrothereua nubila	DNA101791	Costa Rica	FJ660704	FJ660744–5	FJ660785	FJ660817	FJ660841	FJ660872
Dendrothereua homa	DNA102576	Arizona	FJ660705	FJ660746	FJ660786	FJ660818	FJ660842	FJ660873
Scutigera coleoptrata	DNA100198	USA, MA	DQ222123	DQ222140	DQ222155	–	DQ222187	–
Scutigera coleoptrata	DNA100258	USA, NY	AF173238	AF173269	AF370859	DQ222169	DQ222188	–
Scutigera coleoptrata	DNA100259	South Africa	DQ222124	DQ222141	DQ222156	DQ222170	DQ222189	FJ660874
Scutigera coleoptrata	DNA101976	USA, CA	FJ660706	FJ660747	FJ660787	–	FJ660843	FJ660875
Scutigera coleoptrata	DNA102327	Turkey	FJ660707	FJ660748	FJ660788	–	FJ660844	FJ660876
Scutigera coleoptrata	DNA102328	Georgia	FJ660708	FJ660749	–	FJ660819	FJ660845	FJ660877
Scutigera coleoptrata	DNA102329	Georgia	FJ660709	FJ660750	FJ660789	–	FJ660846	FJ660878
Scutigera coleoptrata	DNA102367	Bulgaria	FJ660710	FJ660751	FJ660790	–	FJ660847	FJ660879
Scutigera coleoptrata	DNA102368	Bulgaria	FJ660711	FJ660752	FJ660791	FJ660820	FJ660848	FJ660880
Scutigera coleoptrata	DNA102577	Elba	FJ660712	FJ660753	FJ660792	–	FJ660849	FJ660881
Scutigera coleoptrata	DNA102578	France	FJ660713	FJ660754	FJ660793	–	FJ660850	FJ660882
"Scutigera" nossibei	DNA102102	Madagascar	FJ660714–5	FJ660755	FJ660794	FJ660821	FJ660851	FJ660883
Tachythereua sp.	DNA102575	Senegal	FJ660716	FJ660756	FJ660795	–	FJ660852	FJ660884
Scutigeridae, Thereuoneminae								
Allothereua bidenticulata	DNA101589	NSW	FJ660717	FJ660757	FJ660796	FJ660822	–	FJ660885
Allothereua linderi	DNA101463	NSW	DQ222128	DQ222147	DQ222160	DQ222174	DQ222195	FJ660886
Allothereua linderi	DNA101979	Victoria	FJ660718–9	FJ660758	FJ660797	–	FJ660853	FJ660887
Allothereua maculata	DNA101982	WA	FJ660720	FJ660759	FJ660798	FJ660823	FJ660854	FJ660888
Allothereua maculata	DNA101983	WA	FJ660721	FJ660760	FJ660799	FJ660824	FJ660855	FJ660889
Allothereua maculata	DNA101986	WA	FJ660722	FJ660761	FJ660800	FJ660825	FJ660856	FJ660890
Allothereua maculata	DNA101987	WA	FJ660723	FJ660762	FJ660801	FJ660826	–	FJ660891
Allothereua maculata	DNA101988	WA	FJ660724	FJ660763	FJ660802	FJ660827	FJ660857	FJ660892
Allothereua serrulata	DNA100262	NSW	DQ222129	DQ222148	DQ222161	DQ222175	DQ222197	FJ660893
Allothereua serrulata	DNA101045	QLD	DQ222130	FJ660764	DQ222162	DQ222176	DQ222198	–
Parascutigera festiva	DNA100635	New Caledonia	AY288688	FJ660765	–	DQ222177	DQ222199	FJ660894
Parascutigera festiva	DNA102584	New Caledonia	FJ660725	FJ660766	FJ660803	FJ660828	FJ660858	FJ660895
Parascutigera guttata	DNA102317	QLD	FJ660726	FJ660767	FJ660804	FJ660829	FJ660859	FJ660896
Parascutigera guttata	DNA101971	QLD	FJ660727	FJ660768	FJ660805	–	–	–
Parascutigera guttata	DNA101973	QLD	FJ660728–9	FJ660769	FJ660806	–	–	–
Parascutigera latericia	DNA101046	New Caledonia	DQ222131	DQ222150	DQ222164	DQ222178	DQ222200	–
Parascutigera latericia	DNA102123	New Caledonia	FJ660730	FJ660770	FJ660807	FJ660830	FJ660860	–
Parascutigera latericia	DNA102124	New Caledonia	FJ660731	FJ660771	–	FJ660831	–	FJ660897
Parascutigera nubila	DNA103553	New Caledonia	FJ660732	FJ660772	FJ660808	FJ660832	–	FJ660898
Parascutigera nubila	DNA103554	New Caledonia	FJ660733–4	FJ660773–4	–	FJ660833	–	FJ660899
Parascutigera sp. QLD 1	DNA101974	QLD	FJ660735	FJ660775	FJ660809	FJ660834	FJ660861	FJ660900
Parascutigera sp. QLD 2	DNA101972	QLD	FJ660736	FJ660776	FJ660810	–	FJ660862	FJ660901
Parascutigera sp. QLD 3	DNA101977	QLD	FJ660737	FJ660777	FJ660811	FJ660835	FJ660863	FJ660902
Parascutigera sp. QLD 3	DNA101978	QLD	FJ660738	FJ660778	FJ660812	FJ660836	FJ660864	FJ660903
Parascutigera cf. *sphinx*	DNA101985	WA	FJ660739	FJ660779	–	FJ660837	FJ660865	FJ660904
Parascutigera cf. *sphinx*	DNA101980	WA	FJ660740	FJ660780	FJ660813	FJ660838	FJ660866	FJ660905
Parascutigera cf. *sphinx*	DNA101981	WA	FJ660741	FJ660781	FJ660814	FJ660839	FJ660867	FJ660906
Pilbarascutigera incola	DNA101997	WA	FJ660742	FJ660782–3	FJ660815	–	FJ660868	FJ660907
Thereuonema tuberculata	DNA101632	Japan	DQ222126	DQ222145	DQ222158	DQ222173	DQ222193	FJ660908

Table 1
(*Continued*)

			18S rRNA	28S rRNA	16S rRNA	COI	H3	12S rRNA
Thereuonema turkestana	DNA101090	Kazakhstan	FJ660743	FJ660784	FJ660816	FJ660840	–	FJ660909
Thereuonema turkestana	DNA101091	Uzbekistan	DQ201417	DQ222144	DQ201423	DQ201427	DQ222192	–
Thereuopoda clunifera	DNA100260	Japan	AF173239	DQ222142	AY288716	DQ222171	DQ222190	FJ660910
Thereuopoda longicornis	DNA101461	Thailand	DQ222125	DQ222143	DQ222157	DQ222172	DQ222191	–
Thereuopodina n. sp.	DNA101462	QLD	DQ222127	DQ222146	DQ222159	–	DQ222194	FJ660911

Asterisks in the 28S rRNA GenBank accession number indicate that the sequence corresponds to the D3 expansion fragment. MA, Massachusetts; NY, New York; CA, California; NSW, New South Wales (Australia); WA, Western Australia; QLD, Queensland. Dashes (–) indicate missing fragments; asterisk (*) denotes sequence from GenBank instead of from specimen MCZ DNA100280.

Table 2
Morphological matrix representing the 62 characters coded for the relationships of selected scutigeromorph species

Species							
Proteroiulus fuscus	?---------	-0--0-00--	----000?0-	0----00002	0-000---0-	0----00-00	00
Lithobius variegatus rubriceps	0-0-00----	-0--0-00--	----00000-	0---000000	0000111110	1100001011	11
Paralamyctes validus	0-0-00----	-0--0-00--	----00000-	0---000000	0000111110	1100111011	11
Anopsobius neozelanicus	0-0-00----	-0--0-00--	----000-0-	0---000000	0000111111	1100111011	11
Craterostigmus tasmanianus	0-0-00----	-0--0-00--	----000-0-	0----00000	0000112112	001-001111	11
Scolopendra viridis	0---00----	-0--0-00--	----00000-	0----00000	0000112112	001-001112	11
Sphendononema guildingii	0010111010	1112121100	0001002110	1110121111	111100000-	0001001011	10
Scutigerina malagassa	100-000001	01000000--	-0-0111110	2001111111	111100000-	0001001011	10
Scutigerina weberi	100-000001	01000000--	-0-0111110	2001111111	111100000-	0001001011	10
Scutigerina cf. *weberi*	100-000001	01000000--	-0-0111110	2001111111	111100000-	0001001011	10
Madagassophora hova	100-000001	0100000111	-000111110	2001111111	111100000-	0001001011	10
Dendrothereua nubila	1010111010	0110110111	-000012111	1110221111	111100000-	0001001011	10
Dendrothereua homa	1010111010	0110110111	-000012111	1110221111	111100000-	0001001011	10
Scutigera coleoptrata	1010111110	2111111100	0000002121	1100221111	111100000-	0001001011	10
"*Scutigera*" *nossibei*	1010111110	2111111100	0000002110	1100221111	111100000-	0001001011	10
Tachythereua sp.	1010111110	211?1110--	00-0102010	1100221111	111100000-	0001001011	10
Thereuonema tuberculata	1010111110	2111111120	0000002010	1110221111	111100000-	0001001011	10
Thereuonema turkestana	1010111110	2111111120	0000002010	1110221111	111100000-	0001001011	10
Thereuopoda clunifera	1111111110	2111111100	1001002010	1100221111	111100000-	0001001011	10
Thereuopoda longicornis	1111111110	2111111100	1001002010	1100221111	111100000-	0001001011	10
Thereuopodina n. sp.	1010111110	2111111100	0000002010	1100221111	111100000-	0001001011	10
Pilbarascutigera incola	1010111110	2111111100	1000002010	1100221111	111100000-	0001001011	10
Allothereua bidenticulata	1010111110	2111111110	0100002010	1110221111	111100000-	0001001011	10
Allothereua linderi	1010111110	2111111110	0100002010	1110221111	111100000-	0001001011	10
Allothereua maculata	1010111110	2111111110	0100002010	1100221111	111100000-	0001001011	10
Allothereua serrulata	1010111110	2111111111	0110002010	1110221111	111100000-	0001001011	10
Parascutigera festiva	1010111110	2111110111	-100002010	1110221111	111100000-	0001001011	10
Parascutigera guttata	1010111110	2111110100	-100002010	11A0221111	111100000-	0001001011	10
Parascutigera latericia	1010111110	2111110111	-100002010	1110221111	111100000-	0001001011	10
Parascutigera nubila	1010111011	2111110110	-000002010	1110221111	111100000-	0001001011	10
Parascutigera cf. *sphinx*	1010111110	2111110110	-100002010	1110221111	111100000-	0001001011	10
Parascutigera sp. QLD1	1010111110	2111110100	-100002010	1100221111	111100000-	0001001011	10
Parascutigera sp. QLD2	1010111110	2111110100	-100002010	1100221111	111100000-	0001001011	10
Parascutigera sp. QLD3	1010111110	2111110100	-100002010	1110221111	111100000-	0001001011	10

Question marks (?) indicate missing data; dashes (-) indicate inapplicable character states; (A) indicates a polymorphism of 0,1.

sampled here differs from the holotype (the sole specimen of *P. sphinx*) in some characters suggestive of separate species status (notably a tendency to cluster thickened spiculae adjacent to bristles: Edgecombe, 2007, fig. 2F), but more detailed study of Western Australian *Parascutigera* is needed to determine if the differences are discontinuous.

For Queensland *Parascutigera*, three specimens of *P. guttata* Verhoeff, 1925 as delimited on the basis of morphology were sequenced. These were collected in the Wet Tropics of north Queensland, including the Atherton Tableland (the source of the Mjöberg/Verhoeff specimens that served as the basis for six nominal species). Additional diversity within *Parascutigera* from north Queensland and central eastern Queensland is sampled by four additional specimens that represent three unnamed species. Because of the inferred sister-group relationship between *Allothereua* and *Parascuti-*

gera in previous molecular studies (Edgecombe and Giribet, 2006), seven additional specimens of *Allothereua* were added to test the monophyly of *Parascutigera*, including the type species, *A. maculata* (Newport, 1844) from its type area (south-west Western Australia). To explore further the amount of molecular variation in species, eight specimens of *S. coleoptrata* were added to three used previously (Edgecombe and Giribet, 2006), including samples from the native (Georgia, Turkey, Bulgaria, Italy, France) and introduced (USA) parts of its extensive geographical range.

Molecular methods for amplification and sequencing of DNA fragments are identical to those described in Edgecombe and Giribet (2006), with the exception of the newly added marker. The mitochondrial 12S rRNA fragment was amplified using the scutigeromorph-specific primers Scuti.12SF (5′-GAG GAA CCT GTC CTG TAA TCG-3′) and Scuti.12SR (5′-GGC GGG CAT ATA TTA GTA CTT TTC-3′). Chromatograms were visualized and contigs were made in Sequencher 4.8 (Gene Codes Corporation, 1991–2007, Ann Arbor, MI, USA, and sequence files were assembled in MacGDE (Linton, 2005) and exported in FASTA format for subsequent analysis.

The 12S rRNA data set contains 43 sequences divided into four fragments; 16S rRNA contains sequences of 55 taxa, each divided into nine fragments; 18S rRNA contains sequences of 61 taxa, each divided into three fragments corresponding to the three amplicons; 28S rRNA contains sequences of 60 taxa, each divided into 19 fragments; COI was amplified for 45 taxa and is divided into three fragments, but this marker amplified for only four out of the 11 specimens of *S. coleoptrata* studied; histone H3 contains sequences of 51 taxa, analysed as a single fragment. The combined molecular data set therefore consists of 39 sequence fragments. All data sets were analysed under dynamic homology, that is, not considering them as pre-aligned.

Phylogenetic analyses

Phylogenetic analyses were conducted in POY ver. 4.0 builds 2870, 2881 and 2885 (Varón et al., 2008) using parsimony under direct optimization (Wheeler, 1996). This new version of POY has been discussed in more detail by Murienne et al. (2008a).

All genes were analysed independently and in combination under a set of ten analytical parameters varying the indel-to-change ratio and the transversion-to-transition ratio in a sensitivity analysis fashion (Wheeler, 1995). One parameter set also explored different costs for opening and extending indels (De Laet, 2005). The morphological characters were weighted in two different ways, either receiving a weight of one each, or receiving a weight equal to the highest molecular cost in the combined analysis of all data.

All phylogenetic analyses were run in a cluster of Dell Blades (eight processors per blade, 32 Gb of RAM) using 20–40 processors. A typical analysis consisted of a timed search (driven search) of 2 h each with up to 100 Wagner trees. The timed search of POY implements a default search strategy that effectively combines tree building with tree bisection and reconnection branch swapping, parsimony ratchet, and tree fusing (see Goloboff, 1999, 2002). A second round of searches was conducted with POY ver. 4.0 build 2885 using the same settings as before, with the addition of the input trees for the sensitivity analysis conducted in the previous searches (sensitivity analysis tree fusing; see Giribet, 2007). Nodal support was calculated via parsimony jackknifing (Farris et al., 1996) after transforming the data to static homology data. Node stability (*sensu* Giribet, 2003) was also assessed and depicted using Navajo rugs over the tree obtained under the optimal parameter set according to a modified incongruence length difference (ILD) measure (Mickevich and Farris, 1981; Farris et al., 1994).

Genetic divergence

Molecular evolutionary analyses were conducted using MEGA ver. 4 (Tamura et al., 2008). Pairwise average *p*-distances and associated standard error were calculated (using the pairwise deletion option for eliminating missing data) for COI for the *Allothereua* clade. Sequences were grouped for Western Australia and eastern Australia/New Caledonia, and average *p*-distances and their associated standard error were calculated within and among groups. Calculations for *S. coleoptrata* COI were limited to four sequences due to the problems we had amplifying this marker for that species. Therefore we assessed genetic variation in the two other mitochondrial markers, 12S rRNA and 16S rRNA. The same methodology was applied for calculating average *p*-distances for other taxa.

Results and discussion

Higher-level relationships

As in previous analyses (Edgecombe and Giribet, 2006), morphology provides one strongly supported grouping that is contradicted by the molecular data and overturned in combined analyses, this being a sister-group relationship between Scutigerinidae and all other Scutigeromorpha (see Edgecombe and Giribet, 2006: 518 for discussion of characters that support this group; also Koch and Edgecombe, 2006). Apart from the node splitting off Scutigerinidae, the strict consensus of morphological data is nearly unresolved when analysed with equal character weights. However, morphology

Table 3
Tree lengths for the different partitions analysed and congruence value (ILD) for the combined analysis of all molecules (ILD MOL) and morphology + 6 molecular loci (ILD TOT) at different parameter sets

Parameter set	rib	h3	12S	16S	COI	MOL	MOR	TOT	ILD MOL	ILD TOT
111	3433	409	648	1592	2663	8796	95	8910	0.005798	0.007856
121	5611	595	985	2489	3726	13767	190	13829	0.026222	0.016849
141	9818	953	1650	4189	5810	22804	380	23389	0.016839	0.025183
211	4607	409	702	1834	2673	10522	190	10653	0.028227	0.022341
221	7524	595	1083	2936	3745	16704	380	16436	0.049150	0.010526
241	14769	953	1825	5082	5811	28464	760	30228	0.000843	0.034008
411	6293	409	765	2199	2671	12521	380	12945	0.014695	0.017613
421	12242	595	1199	3631	3722	21945	760	22891	0.025336	0.032414
441	22774	953	2046	6414	5806	39044	1520	41110	0.026918	0.038847
3221	*6317*	*818*	*1363*	*3316*	*5356*	*17176*	*285*	*17553*	*0.000349*	*0.005583*

Rib, nuclear ribosomal genes (18S and 28S rRNA); h3, histone H3; 12S, 12S rRNA; 16S, 16S rRNA; COI, cytochrome *c* oxidase subunit I; MOR, morphological data; MOL, 6 loci combined; TOT, morphology + 6 loci combined. Optimal ILD value is indicated in italics.

The first numeral used in the parameter set column corresponds to the ratio between indel/transversion and the following two numbers correspond to the ratio between transversion/transition; e.g. 111 is equal weights; 121 corresponds to an indel/transversion ratio of 1 and a transversion/transition ratio of 2 : 1—so indels have a cost of 2, transversions have a cost of 2 and transitions have a cost of 1. For a list of the specific step matrices that this involves see Giribet et al. 2002: App. 4.

exerts an influence in combined analyses by altering some nodes in the molecular cladogram for the same parameter set (see examples below).

For the combined analysis of all data, parameter set 3221 (De Laet, 2005) was identified as optimal—the parameter set that minimizes overall incongruence (Table 3). The closest suboptimal parameter set was 111 (all transformations weighted equally), which was the optimal parameter set in the analyses of Edgecombe and Giribet (2006). Results for each individual partition are not shown, although they are discussed whenever relevant. Analysis of all data combined under parameter set 3221 yielded a single optimal tree at 17 553 weighted steps. This tree, with jackknife support values and selected stability plots, is presented in Fig. 1. The tree shows monophyly of the three scutigeromorph families, Pselliodidae, Scutigerinidae, and Scutigeridae, the latter divided into monophyletic Scutigerinae and Thereuoneminae. Pselliodidae, represented by two individuals of the species *Sphendononema guildingii*, is the sister group to a clade composed of Scutigerinidae and Scutigeridae. Although this clade received a jackknife support value of 82%, monophyly of this group appears only under the optimal parameter set. Most other parameter sets suggest a sister-group relationship of Pselliodidae and Scutigerinidae, sometimes even nested within Scutigeridae, as sisters to a clade composed of *Dendrothereua nubila* and *D. homa*. A similar result was already reported by Edgecombe and Giribet (2006), who found the optimal topology for the interrelationships of the three families under a small set of parameter sets for the combined analysis of all data. However, the new taxon sampling did not improve for either Pselliodidae or Scutigerinidae.

With respect to Scutigeridae, our new study allowed a more detailed exploration of the internal relationships of the family and its two subfamilies. The optimal parameter set shows monophyly of both Scutigerinae and Thereuoneminae. Thereuoneminae is monophyletic for five parameter sets, receiving 67% jackknife frequency (JF hereafter) for the most congruent parameter set (Fig. 1), but Scutigerinae has low jackknife support and is monophyletic under just four parameter sets, one of these ambiguously (Fig. 1). Relationships within Thereuoneminae usually depict two clades, one including the genera *Thereuopoda*, *Thereuopodina*, and *Thereuonema* (informally referred to as the *Thereuopoda* clade), and another including the genera *Allothereua*, *Parascutigera*, and *Pilbarascutigera* (the *Allothereua* clade). Resolution within the *Thereuopoda* clade recognizes monophyly of the genera *Thereuopoda* Verhoeff, 1905, and *Thereuonema* Verhoeff, 1905, both with high jackknife frequencies (98 and 97%, respectively). Within the *Allothereua* clade, two nodes appear in almost every analysis, one uniting the south-west Western Australian species *Allothereua maculata* and *Parascutigera* cf. *sphinx*, and another including all the species from eastern Australia and New Caledonia. *Pilbarascutigera incola* is resolved either as sister to the eastern Australia/New Caledonia *Allothereua* clade (optimal parameter set; Fig. 1) or as sister to the whole *Allothereua* clade (most parameter sets). While all species represented by multiple individuals are monophyletic—with the sole exception of the New Caledonian *Parascutigera latericia* (see Discussion below)—both genera *Allothereua* and *Parascutigera* appear polyphyletic. *Allothereua* forms distinct clades in Western and in eastern Australia. Likewise, *Parascutigera* has a distinct clade in Western Australia and possibly multiple clades in Queensland, of which one is most closely related to a radiation in New Caledonia. While monophyly of New Caledonian diversity is not strongly supported by the data, the optimal

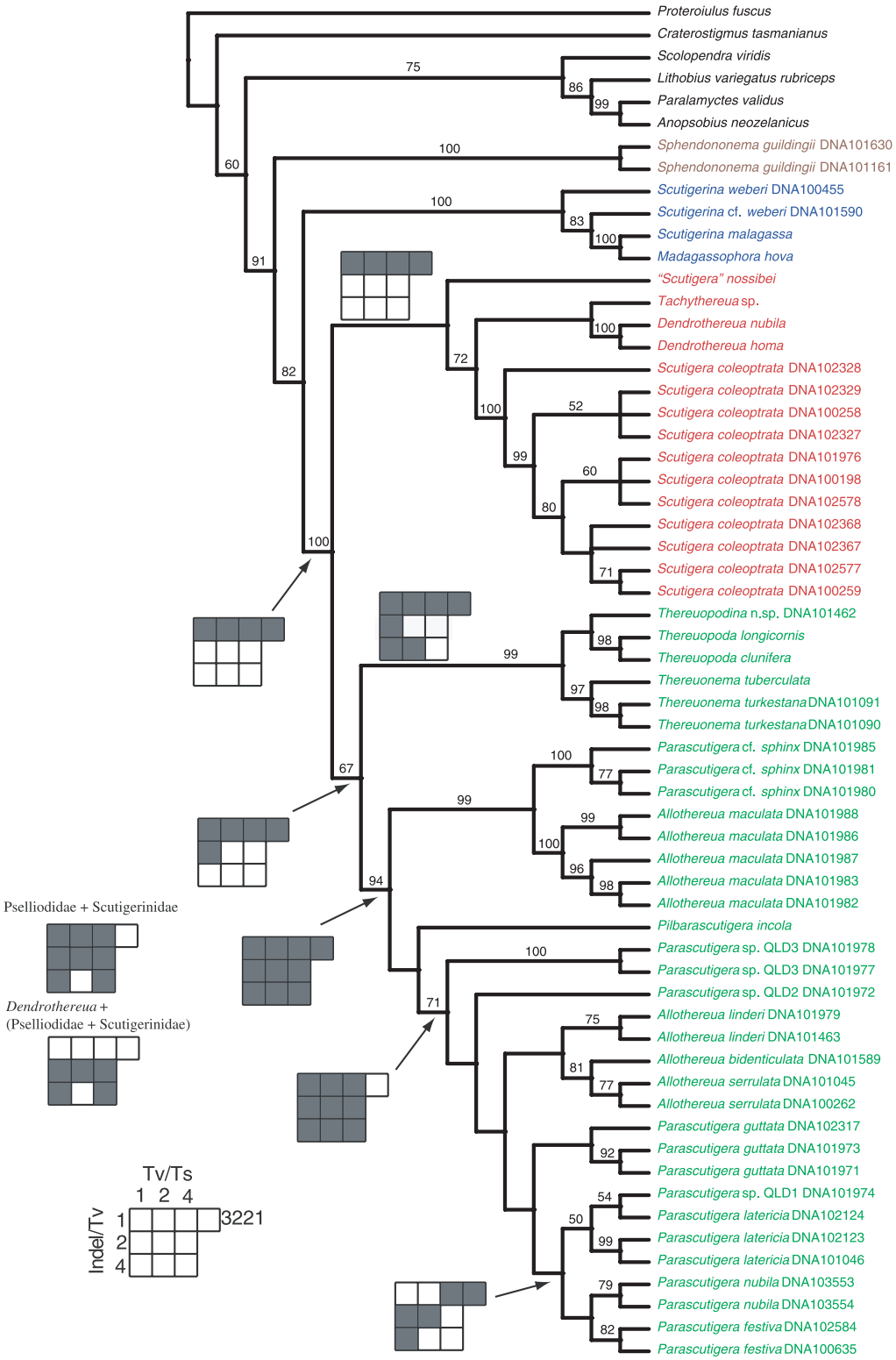

Fig. 1. Total evidence tree for parameter set 3221, the single most parsimonious tree at 17 553 weighted steps obtained after multiple rounds of search and tree fusing. Numbers on branches indicate jackknife frequencies. Navajo rugs indicate the stability of clades to parameter set variation, with transversion-to-transition ratio on the *x* axis (Tv/Ts) and indel-to-change ratio on the *y* axis (Indel/Tv). Pselliodidae appear in brown, Scutigerinidae in blue, Scutigeridae/Scutigerinae in red, and Scutigeridae/Thereuoneminae in green.

Fig. 2. Habitus photographs of *Parascutigera guttata* (Verhoeff, 1925). (A) QM S83809, ♂, body length 20 mm; (B) QM S38746, ♂, body length 22 mm.

parameter set retrieves a tree that unites all New Caledonian species (*P. festiva*, *P. latericia*, *P. nubila*) plus a Queensland individual (*Parascutigera* sp. DNA101974). This clade receives little jackknife support although it is found under some of the most congruent parameter sets.

Parascutigera sp. DNA101974 from Queensland and *P. latericia* DNA102124 from New Caledonia form a clade in all the combined analyses. They appear well supported based on the COI data, with only four nucleotide differences between their haplotypes. This indicates that the two sequences are very closely related, with a level of variability in the range of conspecifics in other scutigeromorph species examined, but that there is no chance for contamination. Morphologically, the Queensland specimen is readily distinguished from *P. latericia* by having pigmentation more like that of *P. guttata* (Fig. 2), that is, predominantly grey rather than brick red longitudinal bands on the tergal plates, much shorter paired spines at the bases of bristles on the tergal plates (cf. T1 in Ribaut, 1923; fig. 17), and a wider sinus in the female gonopods (Fig. 3F versus Ribaut, 1923; fig. 20). Interestingly, the combined analysis of three ribosomal genes (18S, 28S, and 12S rRNA) support a relationship between these two specimens with *ca.* 90% bootstrap support. Nevertheless, original sequences for 16S rRNA and histone H3 for *P. latericia* DNA102124 resulted in contamination from other scutigeromorph species and were excluded from the analyses, and we must therefore view this putative relationship sceptically. The presence of contaminants may be due to poor-quality template DNA.

Relationships among members of Scutigerinae are, for the most part, more unstable and poorly supported than is the case for Thereuoneminae. Four lineages appear in all the analyses, including a clade composed of the 11 specimens of *S. coleoptrata*, a clade including the two *Dendrothereua* species, *Tachythereua*, and "*Scutigera*" *nossibei*. Monophyly of the subfamily as delineated above (minimally uniting those species conventionally assigned to *Scutigera* in the same subfamily, that is, the least inclusive clade including "*S.*" *nossibei* and *S. coleoptrata* in Fig. 1, corresponding to *Scutigera sensu* Lawrence, 1960; Würmli, 1977) is found under four parameter sets (one of which is ambiguous), but these include the two lowest ILD values. The rest of the parameter sets favour different forms of paraphyly of Scutigerinae. This is not surprising because the group lacks any straightforward morphological apomorphies; the traditional distinction between Scutigerinae and Thereuoneminae, presence or absence of distal spine bristles on the first tarsal segment, groups Scutigerinae on the basis of plesiomorphy (the spine bristles being present in Scutigerinidae and Pselliodidae). The Malagasy "*Scutigera*" *nossibei* is the most "divergent" member of the group, and always appears at the base of the subfamily or at the base of a clade that includes Scutigerinae, the *Thereuopoda* clade, and the families Pselliodidae and Scutigerinidae (trees not shown). Maintaining the monophyly of *Scutigera* in light of paraphyly caused by "*S.*" *nossibei* under several parameter sets could require the re-establishment of *Lassophora* Verhoeff, 1905, a genus placed in synonymy with *Scutigera* when its type species, *Lassophora madagacariensis* Verhoff, 1905, was identified as being based on immature specimens of "*Scutigera*" *nossibei* (Würmli, 1975).

Species-level and within-species genetic variation

The molecular evolutionary analysis for the Western Australian *Allothereua* clade for COI showed an average *p*-distance of 0.090 (SE 0.007), while it is 0.133 (SE 0.007) for the eastern Australia/New Caledonia clade. The average *p*-distance between the two groups is 0.146 (SE 0.008). Values for the four COI sequences of *S. coleoptrata* range from 0.003 to 0.150, comparable with those observed for the multiple species within the *Allothereua* clade. One sequence, DNA102328 (from Georgia), presents a large number of differences from the other sequences (also observed in other markers) and is responsible for most of the average *p*-distance observed within the species: 0.027 is observed among the three sequences DNA100258 [Eastern USA],

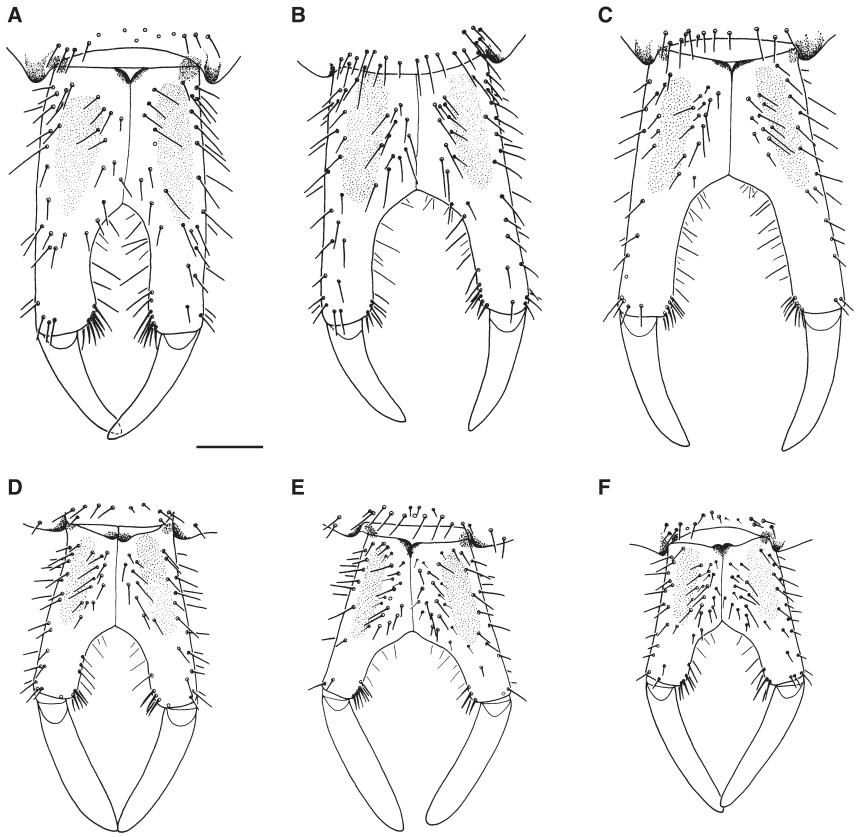

Fig. 3. Variability in female gonopods in *Parascutigera* from Queensland, Australia. (A–C), *Parascutigera guttata* (Verhoeff, 1925). (A) QM S83803, Bellenden Ker Range (body length 21 mm). (B) QM S83810, Hahn Tableland (24 mm). (C) QM S38986, Mt Lewis (20 mm). (D, E) *Parascutigera* QLD 2. (D) QM S37596, Mt Cleveland (19 mm); (E) QM S83812, Mt Pollux (19 mm). (F) *Parascutigera* QLD 1, QM S83811, Pine Mt (20 mm). Scale for all 0.25 μm.

DNA100259 [South Africa] and DNA102368 [Bulgaria], while an average of 0.143 is found among these three and the Georgia sample. In fact, all markers examined for which this Georgian sample has been amplified show DNA102328 as the sister to all other *S. coleoptrata*, the latter clade including a second sample from Georgia (DNA102329) which never groups with DNA102328. This result indicates that *S. coleoptrata* contains an unusual genetic diversity detected within Georgia.

In order to investigate further the genetic structure of *S. coleoptrata*, we calculated their average *p*-distances of 16S rRNA (n = 10; ranging from 0.000 to 0.011) and 12S rRNA (n = 9; ranging from 0.000 to 0.119). The sequences were pooled in three groups according to our phylogenetic results: (i) DNA102328; (ii) DNA100258 (Eastern USA), DNA102327 (Turkey), DNA102329 (Georgia); (iii) DNA100198 (Eastern USA), DNA100259 (South Africa), DNA101976 (Western USA), DNA102367 (Bulgaria), DNA102368 (Bulgaria), DNA102577 (I. Elba), DNA102578 (France) (see Table 1 and Appendix 1 for details). We then calculated the average *p*-distances within and among groups for the two mitochondrial ribosomal markers. 12S rRNA showed more genetic diversity than 16S rRNA, and although it had low internal divergence values for the two groups with more than a single sequence, average *p*-distances among groups ranged between 0.017 and 0.103. 16S rRNA did not amplify for DNA102328, and divergence among the other two groups was low (0.009). The phylogenetic pattern shown by our data clearly illustrates that there is no biogeographical pattern in the specimens sampled, therefore suggesting anthropogenic introductions of the species in recent times. However, the genetic divergence observed in the species is large, and detailed study of multiple individuals per sampling site may be needed to better understand the distribution of the most widespread species of Scutigeromorpha.

Taxonomic discussion

The taxonomy of Scutigeromorpha at the specific and supraspecific levels has been plagued by uncertainty about the diagnostic value of varied morphological characters. A large number of species, most of the genera, and some of the suprageneric groups date back

to work by K. W. Verhoeff published between 1904 and 1944. Even as Verhoeff was establishing his system for the group, his contemporaries were pointing out within-population, ontogenetic and geographical variability on a scale that cast doubt on parts of Verhoeff's taxonomy (Muralevič, 1910; Chamberlin, 1920). The prevailing tendency in subsequent work on Scutigeromorpha is to broadly synonymize species (Würmli, 1977, 1979, 2005), coupled with an acknowledged difficulty in circumscribing the genera (Würmli, 1979). One of the objectives of our study has therefore been to apply molecular sequence data to phylogenetic and taxonomic questions at and above the species level, not least to evaluate the extent to which traditional morphologically delimited taxa correspond to clades. We draw on examples wherein once narrowly split species were subsequently united as a single geographically widespread species (see discussion of *Dendrothereua* below), an example in which putative narrow-range endemics have not yet been subjected to taxonomic revision (*Parascutigera* below), and an example in which genera that have been considered to have widespread distributions throughout the Australian region and Southeast Asia are shown to be non-monophyletic, and thus to define artefactual areas of endemism (*Allothereua* and *Parascutigera* below).

Dendrothereua *and the status of Neotropical Scutigerinae*

One of the anomalies of scutigeromorph distributions is the purported presence of a species of *Scutigera* throughout a broad expanse of the Neotropics, a region whose northern part otherwise lacks native Scutigeridae. We have examined material of "*S. linceci*" from the perspective of both morphology and sequence data, and recognize this taxon as a distinctive scutigeromorph lineage for which we resurrect the generic name *Dendrothereua* Verhoeff, 1944.

Specimens sequenced herein from Costa Rica and Arizona correspond to *Scutigera nubila* Chamberlin, 1922, and *Scutigera homa* Chamberlin, 1942, respectively. Both of these nominal species were considered to be synonyms of *Cermatia linceci* Wood, 1867 by Kraus (1954), Würmli (1973a) and Würmli and Negrea (1977), all of whom advocated an assignment to *Scutigera*. Originally established for material from Texas (Wood, 1867), *S. linceci* has been assigned collections from Costa Rica (Pocock, 1895), Guatemala (Chamberlin, 1944), El Salvador (Kraus, 1954), and Cuba (Würmli and Negrea, 1977). In addition to *S. nubila*, several other species have been placed in synonymy with *S. linceci* (Würmli, 1973a; Würmli and Negrea, 1977), such that its distribution additionally includes Mexico, Nicaragua, and other parts of the southern USA. Under this concept, *S. linceci* is envisioned to be widespread from Texas to Panama (Minelli, 2006).

Although *S. linceci* as delimited by Würmli (1973a) is demonstrably monophyletic on the basis of distinctive morphological autapomorphies (e.g. dense, slender spicula on the tergal plates; narrow sinus between the mesarthron of the female gonopod; short metarthron), and specimens from divergent parts of its range group as a clade with JF 100% (*Dendrothereua* in Fig. 1), we are exceedingly doubtful that a single species is represented. Average *p*-distance for the COI marker in the two specimens of *Dendrothereua* we examined is 0.159 (SE 0.012), more than that found within *S. coleoptrata* or among all the species of *Allothereua/Parascutigera*. Further study of the morphological (e.g. marked differences in pigmentation) and genetic variation within this genus is desired before settling this taxonomic matter. Because the types of *S. linceci* are lost, and a neotype has not yet been designated, we apply the oldest available names for species-group taxa from the areas where the molecular specimens were collected, *S. nubila* Chamberlin, 1922, for Costa Rica, and *S. homa* Chamberlin, 1942, from Arizona.

The assignment of this group to *Scutigera* in its most recent treatments (Würmli, 1973a; Würmli and Negrea, 1977) was not defended. A single apomorphic character that is consistent with classification as *Scutigera* is the alternating presence and absence of tarsal papillae on consecutive tarsomeres of the legs (character 30 in Appendix 2). In contrast to this, however, other morphological characters discussed below are inconsistent with membership in Scutigerinae or even Scutigeridae and, as a consequence, *Scutigera*. Combined analysis with sequence data finds the alliance of the Neotropical group and *S. coleoptrata* to be sensitive to analytical parameters; although the optimal parameter sets are consistent with monophyly of *Scutigera* apart from the nesting of *Tachythereua* within it (Fig. 1), several suboptimal parameter sets ally the Neotropical clade with Pselliodidae and Scutigerinidae rather than with *Scutigera* or any other Scutigeridae. In light of the labile position of this group and its morphological deviation from all scutigerid genera (outlined below), we employ the available name *Dendrothereua* Verhoeff, 1944 for it. The type species, *Dendrothereua arborum* Verhoeff, 1944, from Costa Rica, has been confidently identified by Würmli (1973a) as synonymous with *Scutigera nubila*, a species for which we have examined the holotype (Chamberlin, 1922) and confirm its identity with our sequenced sample from Costa Rica.

Characters of the epipharynx (Fig. 4) and hypopharynx display a unique combination in *Dendrothereua*. As in Scutigerinidae and Pselliodidae, the proximal fork of the hypopharynx lacks a lateral bulge (Koch and Edgecombe, 2006; figs 1a, 2e) that is shared by all members of Scutigeridae examined apart from *Parascutigera nubila*. All other members of Scutigeridae have a pair of sensilla in the medial group of a tripartite cluster

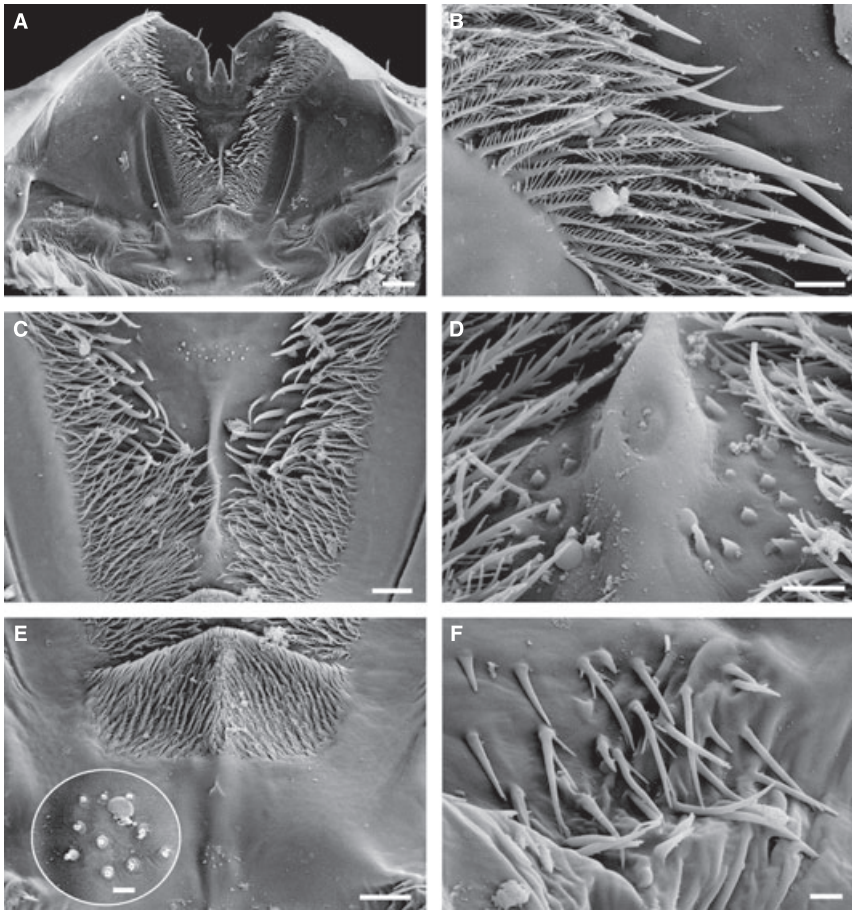

Fig. 4. *Dendrothereua nubila* (Chamberlin, 1922). Epipharynx. (A) Scale 50 μm; (B) labral bristles, scale 10 μm; (C) labral part of epipharynx, scale 20 μm; (D) sensilla at proximal end of median ridge on labral part of epipharynx, scale 5 μm; (E) clypeal part of epipharynx, scale 20 μm; inset, sensilla on median part of clypeal triangle, scale 2 μm; (F) spine cluster on lateral clypeal part of epipharynx, scale 5 μm.

on the proximal labral part of the epipharynx arranged as a side-by-side pair (Koch and Edgecombe, 2006; figs 6c, 8e), whereas in *Dendrothereua* these sensilla are aligned anteroposteriorly (Fig. 4D). The anteroposterior alignment of these sensilla is uniquely shared with the two genera of the Scutigerinidae, *Scutigerina* and *Madagassophora* (Koch and Edgecombe, 2006; fig. 8a). In all other Scutigeridae, the labral trapezoid is fringed by a single row of pectinate bristles laterally, with an abrupt transition to a wider field of longer simple bristles. In contrast, in *Dendrothereua* a few rows of branching bristles are present laterally and the inner row of simple bristles is single (Fig. 4B, C). This condition is unique within Scutigeromorpha.

Another distinctive character of *Dendrothereua* compared with Scutigeridae is the presence of dense hairs on the sternites and coxae of posterior trunk segments—hairs in addition to the (articulated) bristles that are present in all scutigeromorphs. The dense covering of hairs is uniquely shared with Scutigerinidae (Lawrence, 1960; fig. 31b; Edgecombe and Giribet, 2006; fig. 4E) and was previously optimized as an autapomorphy of that family. On the tergal plates, the absence of unpaired spines associated with a bristle is a difference from *Scutigera* and most members of the family Scutigeridae, as well as Pselliodidae. The tergal prominences are confined to bristles and spicula, the latter being long (about half the length of a bristle) and hair-like (Würmli, 1973a; fig. 1).

Analysis of the morphological data on their own under implied weights ($k = 2$ or 3) resolves *Dendrothereua* as sister group of all other Scutigeridae, though this is one of a broader range of equally parsimonious hypotheses under equal weights. A basal position in Scutigeridae is influenced by the putatively plesiomorphic characters shared with Scutigerinidae (arrangement of epipharyngeal sensilla; sternal and coxal hairs) or Scutigerinidae + Pselliodidae (absence of lateral bulge in the proximal fork of the hypopharynx).

Classification of *Dendrothereua* species as a single species of *Scutigera* has almost certainly underestimated species diversity in the Neotropics and obscures a

biogeographical signal that this region harbours a clade that morphology and many combined parameter sets identify as non-scutigerine.

Allothereua *and* Parascutigera

Much of the diversity depicted in Fig. 1 involves *Allothereua* and *Parascutigera*, two genera that were originally classified in separate tribes (Verhoeff, 1905), but were found to be each other's closest relative when subjected to cladistic analysis of molecular and morphological data (Edgecombe and Giribet, 2006). This hypothesis suggests that most Australian scutigeromorph diversity is, on the whole, more closely allied than was originally thought. Whether the two genera are themselves monophyletic could not be tested very severely because of the limited taxonomic sampling in our previous study, but is of biogeographical interest because both genera describe putative areas of endemism throughout the Australian–Asian regions. *Parascutigera* is purported to be represented by species in New Britain (Papua New Guinea) (Verhoeff, 1904), the Philippines (Chamberlin, 1921), the Malay Peninsula (Verhoeff, 1937), and Lembeh in North Sulawesi (Chamberlin, 1944), in addition to its six nominal species in Queensland (Verhoeff, 1925), one in Western Australia (Verhoeff, 1925), and five nominal species in New Caledonia (Ribaut, 1923; Würmli, 1974a). In addition to its Australian taxa, *Allothereua* has been assigned species from Kazakhstan, Nepal, and the Philippines (Edgecombe and Giribet, 2006).

The distinction between *Parascutigera* and *Allothereua* has hinged on a single morphological difference, whether unpaired spines are (*Allothereua*) or are not (*Parascutigera*) developed in association with a bristle on the tergal plates. Given that both of these states are observed in other scutigeromorph genera, it might be expected that either *Allothereua* or *Parascutigera* could be paraphyletic with respect to the other. Monophyly of the *Allothereua* + *Parascutigera* group is strongly corroborated by the present findings. This group, with the monotypic *Pilbarascutigera* either as sister or an internal member (Fig. 1), is monophyletic across all explored parameters. For the molecular data alone, the most congruent parameter set (3221) supports an *Allothereua–Parascutigera* clade that excludes *Pilbarascutigera*, which is then its sister (as is likewise found for most suboptimal parameter sets for the combined data). Irrespective of the position of *Pilbarascutigera*, however, neither *Allothereua* nor *Parascutigera* in its traditional, morphologically defined sense is monophyletic—both are in fact polyphyletic. This is perhaps not altogether surprising, because the assignment of a species to *Allothereua* hinges on the unpaired spine/bristle association noted above, in some cases this being restricted to only one or two tergal plates (TT6–7) and only a few such spines.

Until the type species of *Parascutigera*, *P. dahli* Verhoeff, 1904 from New Britain, is appraised molecularly, we abstain from formal reclassification of *Allothereua* and *Parascutigera*. Species are depicted in Fig. 1 according to their traditional classification based on spine/bristle associations on the tergal plates to highlight the pattern of non-monophyly of the genera. Particularly clear-cut is the affinity of *Parascutigera* cf. *sphinx* to the type species of *Allothereua*, *A. maculata*, both of which inhabit south-western Western Australia. This clade is found across all explored parameter sets with a JF of 99% for the optimal parameter set for the combined data. It is also found for the independent analysis of all the ribosomal partitions. A comparable nesting of *Allothereua* species (a clade including *A. bidenticulata*, *A. linderi* and *A. serrulata*) within a grade of *Parascutigera* species is retrieved within eastern Australia. Assuming that the type species of *Parascutigera* proves to be related to geographically proximal diversity with that genus (e.g. the clade uniting north Queensland and New Caledonian species in Fig. 1), the south-eastern Australian taxa now assigned to *Allothereua* may best be transferred to *Parascutigera*, should the two genera be deemed worthy of retention.

Species-level variability: testing for narrow-range endemism

The six species of *Parascutigera* established by Verhoeff (1925) from a few sites on the Atherton Tablelands of north Queensland, Australia, provide an opportunity to access the case for narrow range endemism in these centipedes. The sample size represented by the six putative species is 14 specimens in total (three species having been based on their holotype alone, and two of those being known solely from the more taxonomically uninformative male).

The deep nodes of Verhoeff's (1925: 20–22) key to Australian *Parascutigera* species employed a set of morphological characters to which he ascribed diagnostic value for segregating species or groups of species. Purportedly informative characters involving pigmentation of the legs and colour of the stoma saddles (swollen areas of the tergal plates above the spiracles) are critiqued in the Appendix 3, in discussion of what we regard to be a single species to which the name *Parascutigera guttata* Verhoeff, 1925 is applied.

At the shallower nodes in his key (separating species), Verhoeff placed considerable emphasis on the proportions of the female gonopods, including the relative lengths of the distal sectors known as the mesarthron and metarthron (Würmli, 1974b), divergence or not of the mesarthron, and the shape of the sinus between the inner margins of the mesarthron (horseshoe-shaped,

more or less elliptical, or triangular) (see Bolton et al., 2009 for a geometric morphometric approach to gonopod descriptions). Most of this variation was depicted in the figured gonopods of *P. noduligera* (Verhoeff, 1925; pl. 1, fig. 3) and *P. guttata* (Verhoeff, 1925; pl. 1, fig. 3). The proportions regarded by Verhoeff as diagnostic of species are observed to display continuous variation across a larger sample of specimens, with examples selected to show variation in Fig. 3A–C. These include gonopods as depicted for *P. guttata* (Fig. 3B) and *P. noduligera* (Fig. 3A). Large maturus stage individuals typically have a relatively short metarthron, the mesarthon being up to 1.24 times the length of the metarthon (Fig. 3A). However, other large individuals that resemble "short-metarthron" specimens in having a narrow sinus (*mjoebergi*- or *noduligera* type gonopods of Verhoeff) have the mesarthon as little as 76% the length of the metarthon. Within a single population, much of the variation in mesarthron/metarthon length noted above can be observed. The specimens depicted in Figs 3B and C are molecular vouchers *P. guttata* DNA101971 and DNA101973, resolved in Fig. 1 as each other's closest relative, and *P. guttata* as delimited morphologically is monophyletic.

Viewed as a single species, the extent of variability in the gonopods of north Queensland *Parascutigera* is considerably less than that in *Thereuopoda longicornis* and *T. clunifera* (both *sensu* Würmli, 1979), or *Scutigera coleoptrata sensu* Würmli, 1977, in which many nominal species established largely on the basis of female gonopod proportions were subsequently identified as single variable, widespread species. Though we are thus sceptical that gonopod shape can be used to identify multiple species within the Wet Tropics region of north Queensland, gonopods corroborate molecular evidence that multiple species of *Parascutigera* can be identified over a broader geographical scale in Queensland. Notably, specimens from central eastern Queensland (including those used in the molecular analyses) can be distinguished morphologically from *P. guttata* by the relatively wide sinus between the margins of the mesarthron (Fig. 3D–F) as well as a relatively long metarthron. Specimens with this gonopod morphology are assigned to *Parascutigera* QLD 1 and 2 in the cladograms, and are found to cluster separately from *P. guttata* in all analyses (Fig. 1).

The Australian–New Caledonian biogeographical split

Our data clearly support a split in the *Allothereua* clade between the species from south-western Australia and those from eastern Australia/New Caledonia (Fig. 5). The latter form a clade in which eastern Australia appears paraphyletic with respect to New Caledonia. Whether the New Caledonian species constitute a clade or not is still debatable, given the support from the data presented

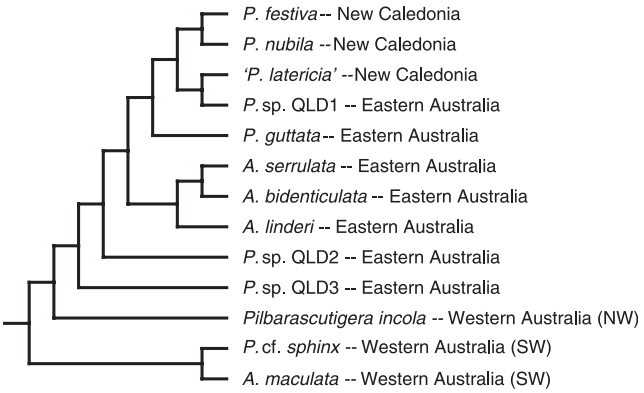

Fig. 5. Taxon-area cladogram for the *Allothereua–Parascutigera* clade, summarizing relationships in Fig. 1. Generic assignments follow traditional taxonomy, abbreviated A (*Allothereua*) and P (*Parascutigera*). "New Caledonia" as plotted here represents widespread distributions on Grande Terre. Taxa in Western Australia occur in the south-west forests (SW) and Pilbara and Kimberley (north-west, NW).

here. What is interesting from a biogeographical point of view is the strong support for a clade that unites species from parts of Australia with those from other continental fragments to the exclusion of other Australian species, as suggested in a previous study on lithobiomorph centipedes that divided Australia into micro-areas for biogeographical analyses (Giribet and Edgecombe, 2006). A vicariant split between western and eastern Australia is also evident in animals of low vagility, such as the cyphophthalmid Opiliones family Pettalidae (Boyer and Giribet, 2007), although in this case no connection exists between the Cyphophthalmi from eastern Australia and the endemic family Troglosironidae of New Caledonia (Boyer et al., 2007).

New Caledonia is at the margin of the Australian and Pacific plates, 1200 km east of Queensland and 1700 km north of New Zealand in the south-west Pacific. It is currently at the forefront of biogeographical discussions in the south-west Pacific (Ladiges and Cantrill, 2007), being treated as either a continental island that originated by an amalgamation of terranes, some of which may pre-date Gondwana, with an ancient biota or, alternatively, as a recently re-emerged land mass analogous to a Darwinian island hosting long-distance recent dispersers (see reviews in Grandcolas et al., 2008; Heads, 2008). The three New Caledonian species of *Parascutigera* used in this study are all widespread on Grande Terre, and the individuals selected for sequencing are from widely separated localities; each species occupies multiple terranes in the seven-terrane scheme for Grande Terre described by Heads (2008). A relationship between Australian and New Caledonian biotas is likewise evident in the centipede genera *Henicops* and *Dichelobius*, although in those cases the New Caledonian species appear more closely related to

those from south-west Western Australia than to those from Queensland (Edgecombe and Giribet, 2003, 2004; respectively). The beetle genus *Papuadytes* is found in Australia, New Guinea, and New Caledonia, and at least one New Caledonian clade has its sister in Australia, although towards the centre of the continent, in the Northern Territory, with Australia also representing several basal lineages within the genus (Balke et al., 2007). In the case of the southern beech *Nothofagus*, the New Caledonian species are closest to those of New Guinea (Heads, 2006), while many insect genera/families are wholly endemic (e.g. Murienne et al., 2005, 2008b), or have widespread distributions that include the surrounding territories (e.g. Aguiar and Jennings, 2007; Pratt et al., 2008; Trewick et al., 2008). Heads (2008) indicated that many groups have eastern Australia–New Caledonia distributions, depicting an example from the orchid *Acianthus* (Heads, 2008; fig. 1), and sister groups between eastern Australia and New Caledonia are observed in various insect taxa, such as the bug genera *Austrovannius* (Cassis et al., 2003) and *Dilatops* (Cassis and Weirauch, 2008). Examples of eastern Australia + New Caledonia distributions appear to be more numerous in the taxonomic literature than are represented by area cladograms.

Concluding remarks

Our novel molecular and morphological data suggest monophyly of the three families of scutigeromorph centipedes, Pselliodidae, Scutigerinidae, and Scutigeridae, the latter probably divided into Thereuoneminae and Scutigerinae. Although evidence for the monophyly for Pselliodidae, Scutigerinidae, and Thereuoneminae is ample from the data analysed, that of Scutigerinae is more questionable. As in our previous study, the data support a sister group of the Afrotropical/Neotropical Pselliodidae to the remainder of the order, although a sister relationship between pselliodids and the southern African/Malagasy Scutigerinidae cannot be ruled out. Likewise, some data suggest that Pselliodidae + Scutigerinidae may be nested within Scutigerinae, as sister to a Neotropical clade (*Dendrothereua*) whose genetic and morphological distinctness has been obscured by its classification as *Scutigera*. This result is, however, obtained only when the rooting of the scutigeromorph tree occurs within Thereuoneminae.

Thereuoneminae is well resolved, and most analyses suggest that *Pilbarascutigera* from arid north-west Western Australia is sister to the *Allothereua/Parascutigera* clade, which is always divided into a south-west Western Australian clade of *Allothereua/Parascutigera* and an eastern Australia/New Caledonian clade of *Allothereua/Parascutigera*. In other cases, *Pilbarascutigera* is sister to the eastern Australia/New Caledonian clade. The analyses therefore show that neither *Allothereua* nor *Parascutigera* in their traditional sense is monophyletic, and the cladogram (but not the classification) depicts a vicariant pattern across Australia as well as tropical Australian affinities for New Caledonian Scutigeromorpha. New Caledonian diversity may derive from a single colonization.

While most species evaluated for multiple specimens are monophyletic, the amount of genetic variation observed in COI (and other mitochondrial markers) varies among species and species-groups. Variation within *S. coleoptrata* is large, but most of the genetic diversity is due to a single specimen from Georgia, and therefore it is unclear whether the sampling of each species is sufficient to estimate the true genetic diversity within scutigeromorph species. Now that the phylogenetic pattern of Scutigeromorpha is beginning to be well established on a broad scale, it may be time to focus on phylogeographical and population genetic studies of selected species in order to comprehend the amount of variation observed in gonopods and other morphological characters traditionally used in scutigeromorph systematics.

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Appendix 1

Voucher details for new specimens used in molecular analyses. Repositories abbreviated as follows: AMNH, American Museum of Natural History; AM KS, Australian Museum; FMNH, Field Museum of Natural History; MCZ, Museum of Comparative Zoology, Harvard University; QM, Queensland Museum; WAM, Western Australian Museum. Previously published samples listed by Edgecombe and Giribet (2006: App. 1).

Scutigera coleoptrata (Linnaeus, 1758).
MCZ DNA101976.
USA: California: La Jolla, 38°43′44″ N 177°09′46″ W, 153 m; x.2006, leg. G. W. Rouse.

Scutigera coleoptrata (Linnaeus, 1758).
MCZ DNA102327.
Turkey: Anamur District: Akçali Daglari Mts., Ovabasi, near Kosekbükü Astim Magarasi Caves, 36°07.638′N 32°45.596′E, 145 m; 15.vii.2006, leg. D. Duhalov, S. Lazarov, P. Stoev.

Scutigera coleoptrata (Linnaeus, 1758).
MCZ DNA102328-102329.
Georgia: Imereti Province: Kutaisi District: Parctskhanaaknevi, 42°11.870′N 42°33.196′E, 107 m; 21.vii.2006, leg. S. Lazarov, P. Stoev.

Scutigera coleoptrata (Linnaeus, 1758).
MCZ DNA102367-102368.
Bulgaria: Yambol District: Deventsky vazvisheniya Highlands, Oman; 27.v.2007, leg. P. Stoev.

Scutigera coleoptrata (Linnaeus, 1758).
MCZ DNA102577.
Italy: Elba: Fetvaia; 26.vii.2007, leg. C.H.G. Müller.

Scutigera coleoptrata (Linnaeus, 1758).
MCZ DNA102578.
France: Dordogne: 1 km N of Margueron, 44°46′38″N 00°16′04″E; x.2007, leg. M. Yeung.

''Scutigera'' nossibei Saussure & Zehntner, 1902.
MCZ DNA102102/FMNH-INS 013 177.
Madagascar: Province Mahajanga: SF d'Ampijoroa, 16°19.4′S 46°48.4′E, 160 m; 18.iv.2003, leg. S. M. Goodman.

Dendrothereua homa (Chamberlin, 1942).
MCZ DNA102576/AMNH LP 5877.
USA: Arizona: Pima County: Vail, Collassal Cave Road, *ca.* 32°02.180′N 110°39.914′W, 1007 m; 20.vi.2006, leg. R. Mercurio, B. Savary.

Dendrothereua nubila (Chamberlin, 1922).
MCZ DNA101790.
Costa Rica: Cascajal de Coronado; 6.x.2005, leg. G. Mayer.

Tachythereua sp.
MCZ DNA102575/AMNH LP 4908.
Senegal: 100 km SW of Kildira, 14°05′14.2″N 16°57′23.1″W; 5.vii.2005. leg. J. Huff, V. Vignoli.

Thereuonema turkestana Verhoeff, 1905
MCZ DNA101090.
Kazakhstan: Talgar District: 6.5 km due N of Kapchagai, E bank of Ili river, 43°57.232′N 77°04.110′E; 8.v.2003, leg. A. V. Gromov, L. Prendini.

Allothereua bidenticulata Verhoeff, 1925
MCZ DNA101589.
Australia: New South Wales: Oatley, 33°58.820′S 151°03.899′E, 38 m; 2004, leg. G. D. F. Wilson.

Allothereua linderi Fahlander, 1939 (= *A. bidenticulata linderi*).
MCZ DNA101979/AM KS 099806.
Australia: Victoria: Yallourn North, 38°08′43″S 146°21′23″E, 100 m; 18.iv.20005, leg. R. Mesibov.

Allothereua maculata (Newport, 1844).
MCZ DNA101982-101983/AM KS 099810.
Australia: Western Australia: Crowea Forest, 34°32′23″S 116°02′30″E, 123 m; 23.i.2006, leg. G. D. Edgecombe, G. Giribet.

Allothereua maculata (Newport, 1844).
MCZ DNA101986/WAM T92365.
Australia: Western Australia: Bryce Road, 1.5 km N of Boyanup, 33°28′12″S 115°43′28″E; 20.xii.2004, leg. M. S. Harvey.

Allothereua maculata (Newport, 1844).
MCZ DNA101987/WAM T92366.
Australia: Western Australia: NE of Augusta on Governor Broome Road, 34°15′05″S 115°22′12″E; 11.iii.2005, leg. M. S. Harvey, J. Waldock, K. Edward.
Allothereua maculata (Newport, 1844).
MCZ DNA101988/WAM T92367.
Australia: Western Australia: Peppermint Park, near Harvey, 33°05′S 115°58′E; 8.vi.2005, leg. A. F. Longbottom, P. J. Mann.
Parascutigera festiva Ribaut, 1923.
MCZ DNA102584.
New Caledonia: Province Nord: Ateou, leg. G. B. Monteith.
Parascutigera guttata Verhoeff, 1925.
MCZ DNA101971/QM S83810.
Australia: Queensland: Hahn Tableland (North End), 16°49′S 145°11′E, 1000 m; 13.xii.1995, G. B. Monteith, D. J. Cook, G. Thompson.
Parascutigera guttata Verhoeff, 1925.
MCZ DNA101973/QM S38986.
Australia: Queensland: Mt Lewis, 16 km from Bushy Ck, 16°34′S 145°16′E, 900 m; 20.iv.1997, leg. G. B. Monteith.
Parascutigera guttata Verhoeff, 1925.
MCZ DNA102317.
Australia: Queensland: Atherton Plateau, Rose Gums Wilderness Retreat, 17°18′51.1″S 145°42′08.6″E, 770 m; 15–16.iii.2006, leg. G. Hormiga, L. Lopardo.
Parascutigera latericia Ribaut, 1923.
MCZ DNA102124.
New Caledonia: Province Sud: Col de Mouirange, 22°13′S 166°41′E, 200 m; 23.xi.2002, leg. G. B. Monteith.
Parascutigera latericia Ribaut, 1923.
MCZ DNA102123.
New Caledonia: Province Nord: Aoupinie, 21°11′S 165°19′E, 850 m; 20.xi.2000, leg. G. B. Monteith.
Parascutigera nubila Ribaut, 1923.
MCZ DNA103553.
New Caledonia: Province Sud: Riverière Bleue (Mois de Mal), 22°07′S 166°39′E, 400 m; 19.xi.2001, leg. G. B. Monteith.
Parascutigera nubila Ribaut, 1923.
MCZ DNA103554.
New Caledonia: Province Nord: Aoupinie top camp, 21°11′S 165°18′E, 850 m; 23.xi.2001, leg. G. B. Monteith.
Parascutigera cf. *sphinx* Verhoeff, 1925.
MCZ DNA101980-101981/AM KS 099807.
Australia: Western Australia: Lane Poole Reserve, S of Dwellingup, 32°45′45″S 116°04′36″E, 176 m, 21.i.2006, G. D. Edgecombe, G. Giribet.
Parascutigera cf. *sphinx* Verhoeff, 1925.
MCZ DNA101985/AM KS 099808.
Australia: Western Australia: Serpentine National Park, 32°24′16″S, 116°05′45′E', 238 m; 21.i.2006, leg. G. D. Edgecombe, G. Giribet.
Parascutigera QLD sp. 1.
MCZ DNA101974/QM S83811.
Australia: Queensland: Pine Mt, 3 km S, 21°46′S 148°51′E, 240 m; 1.vi.2000, leg. G. B. Monteith.
Parascutigera QLD sp. 2.
MCZ DNA101972/QM S83812.
Australia: Queensland: Mt Pollux, eastern slopes, 22°28.6′S 147°52.4′E, 480 m; 6.iii.2006, leg. C. Burwell, G. B. Monteith.
Parascutigera QLD sp. 3.
MCZ DNA101978/AM KS 099812.
Australia: Queensland: Wongabel State Forest, 17°19′57.3″S 145°29′57.9″E, 782 m; 29.v.2006, leg. L. Barrow, G. D. Edgecombe.
Parascutigera QLD sp. 3.
MCZ DNA DNA101977/AM KS 099805.
Australia: Queensland: Curtain Fig Tree National Park, 17°17′14.5″S 145°34′20.4″E, 762 m; 30.v.2006, leg. L. Barrow, G. D. Edgecombe.
Pilbarascutigera incola (Verhoeff, 1925).
MCZ DNA101997/WAM T76701.
Australia: Western Australia: near Cloud Break Mining camp, 22°17′52″S 119°22′52″E; 3.vii.2006, leg. M. S. Harvey.

Appendix 2

Morphological characters coded in Table 2. All characters are described and discussed by Edgecombe and Giribet (2006) apart from characters 2, 21, and 22, introduced by Edgecombe and Barrow (2007).

1. Proportions of antennal articles: (0) as long as wide; (1) much wider than long.

2. Spines on proximal half of first antennal flagellum: (0) absent; (1) present.

3. Anterior (antennal) branch of antennocellar suture: (0) present; (1) absent.

4. Course of projections on cephalic sutures: (0) posterior part subparallel; (1) posterior part divergent.

5. Ventral spine bristle on prefemur of second maxilla: (0) absent; (1) present.

6. Pair of distal spine bristles on tibia of second maxilla: (0) absent; (1) present.

7. Cluster of sensilla at apex of proximal fork in hypopharynx: (0) absent; (1) present.

8. Sclerotized lateral bulge in proximal fork in hypopharynx: (0) absent; (1) present.

9. Groove along lateral bar of labral trapezoid: (0) absent; (1) present.

Previous coding treated either a smooth, narrow groove or a surface of low, rounded tubercles as alternative states of a single character because all examined species displayed one or the other condition (the tubercles then being confined to Scutigerinidae, other scutigeromorphs having a groove; documented by Koch and Edgecombe, 2006). Two characters (nine and ten herein) are now employed because *Parascutigera nubila* Ribaut, 1923, is observed to have tubercles developed along the surface of a groove.

10. Tubercles along lateral bar of labral trapezoid: (0) absent; (1) present.

11. Structure of bristles on labral trapezoid: (0) wide field of pectinate bristles; (1) all simple; (2) narrow outer band of pectinate bristles, wide inner band of simple bristles.

12. Labral trapezoid with two median sensillar clusters: (0) absent; (1) present.

13. Arrangement of tripartite sensilla clusters on proximal labral part of epipharynx: (0) median group between lateral clusters; (1) median group completely distal to lateral clusters.

14. Median sensilla of tripartite cluster on proximal labral part of epipharynx: (0) antero-posteriorly aligned pair; (1) side-by-side pair; (2) diamond-shaped group of four sensilla.

15. Lateral field of spines on clypeal part of epipharynx: (0) absent; (1) present.

16. Position of median sensillar cluster on clypeal part of epipharynx: (0) transverse bands of sensilla immediately proximal to dense median spine field; (1) transversely ovate cluster of sensilla distinctly separated from dense median spine field; (2) transverse bands of sensilla within dense median spine field.

17. Large unpaired tergal spines associated with bristles: (0) absent; (1) present.

18. Tergal spicula (hairs): (0) absent; (1) present.

19. Form of tergal spicula: (0) short triangular spines; (1) setiform, tapering hairs, shorter than bristles; (2) needle-like hairs, as long as bristles.

20. Density of spicula: (0) one spiculum for each of several cuticular polygons; (1) spicula at margins of nearly all cuticular polygons.

21. Kind of bristle paired with spines on TT5–7: (0) *Stachelborsten*; (1) *Tastborsten*.

22. Length of paired spines at bases of bristles (scored for TT6–7): (0) short, flat, triangular spines; (1) elongate, conical spines, often more than half length of bristle.

23. Thickened spicula clustered in patches around bristles and spines: (0) absent; (1) present.

24. Vaulting of stoma saddles: (0) weak or moderate; (1) strong.

25. Median embayment in posterior margin of sternites: (0) shallow or lacking; (1) strong.

26. Coxa and sternites of posterior segments with dense covering of hairs between bristles: (0) hairs absent; (1) hairs present.

27. Carinae on legs: (0) absent; (1) weak; (2) strong. ORDERED

28. Paired spine bristles at end of first tarsal segment: (0) absent; (1) present.

29. Tarsal papillae: (0) absent on all legs; (1) present on legs 1–14; (2) on legs 1–9 only.

30. Distribution of tarsal papillae: (0) present on each consecutive tarsomeres; (1) alternating presence and absence on consecutive tarsomeres.

31. Resilient sole-hairs: (0) absent; (1) single pair with base distomedial to tarsal papilla; (2) two pairs, one with base distomedial to tarsal papilla, one with base proximolateral to papilla.

32. Spine bristles at distal end of tibia: (0) all legs with two spine bristles in 1/1 arrangement; (1) several posterior legs with three spine bristles in 1/2 arrangement.

33. Sinus between inner sides of mesarthron of female gonopod: (0) sinus broad, semicircular or parabolic; (1) sinus deep, narrow, parallel-sided.

34. Single row of coarse spines along inner margin of metarthron of female gonopod: (0) spine row absent; (1) spine row present.

35. Form of male gonopods on first genital segment: (0) segmented; (1) lamelliform; (2) slender styles.

36. Form of male gonopods on second genital segment: (0) absent; (1) blunt cones; (2) slender styles.

37. Maxillary organ: (0) absent; (1) present.

38. Single large tergal plate over trunk segments 7–9: (0) separate plates; (1) single plate.

39. Tarsus form: (0) one or two articles; (1) flagelliform, multiarticulate.

40. Position of spiracles: (0) pleural; (1) dorsal opening on tergum; (2) sternal, at base of legs.

41. Shaft organ on antennal scape: (0) absent; (1) present.

42. Spine comb (*Dornenkamm*) on maxillipede tarsus: (0) absent; (1) present.

43. Projection of hypopharynx as an elongate tongue: (0) short hypopharynx; (1) elongate hypopharynx.

44. Chevron-shaped row of transversely compressed, triangular denticles at border between labral and clypeal parts of epipharynx: (0) absent; (1) present.

45. Flattening of head capsule: (0) domed; (1) flattened.

46. Trochanter on second maxilla: (0) separated from prefemur; (1) fused to prefemur with incomplete articulation.

47. Coxosternite of maxillipede sclerotized in midline: (0) coxae separated in midline; (1) coxosternal plates meeting medially, hinge flexible; (2) midline sclerotized, inflexible. ORDERED

48. Tarsungulum on maxillipede: (0) separate tarsus and pretarsus; (1) tarsus and pretarsus fused.

49. Coxal organs: (0) absent; (1) present.

50. Distribution of coxal organs: (0) on last four pairs of legs; (1) on last two pairs of legs; (2) on last pair of legs only.

51. Single transverse seta projecting medially from labral side piece: (0) absent; (1) present.

52. Plumose setae on inner surface of tarsus of second maxilla: (0) absent; (1) present.

53. Female gonopod and egg manipulation: (0) forcipulate gonopod, used to manipulate single eggs; (1) gonopod lacking, mother humps egg cluster.

54. Form of female gonopod: (0) three articles, the basal article bearing spurs (macrosetae), terminal article with a broad claw; (1) two articles, the proximal article of each gonopod pair partly joined, the distal article a spine.

55. Pleurite of maxilllipede segment: (0) discontinuous ventromedially; (1) continuous ventromedially.

56. Distal spinose projections on anterior side of tibia of legs 1–11: (0) absent; (1) present.

57. Maxillipede segment: (0) with locomotory limb; (1) incorporated into head as maxillipede with fang and poison gland.

58. Maxilllipede tooth plates: (0) absent; (1) present.

59. Special heterotergy: (0) absent; (1) present.

60. Number of post-maxillipede trunk leg pairs: (0) 32–53 trunk rings; (1) 15; (2) 21.

61. Anisostigmophory: (0) spiracles on all pedigerous trunk segments from second segment; (1) spiracles associated with long tergites only.

62. Molar plate on mandible: (0) present; (1) absent.

Appendix 3

Systematic treatment of *Parascutigera guttata* as revised herein.

Parascutigera guttata Verhoeff, 1925.

(Figs 2, 3A–C, 6–8).

Parascutigera guttata Verhoeff, 1925: 22, pl. 1, fig. 4.

Parascutigera aculeata Verhoeff, 1925: 27. *Nov. syn.*

Parascutigera mjoebergi Verhoeff, 1925: 25. *Nov. syn.*

Parascutigera noduligera Verhoeff, 1925: 24, pl. 1, figs 3, 10. *Nov. syn.*

Parascutigera spinulata Verhoeff, 1925: 28. *Nov. syn.*

Parascutigera viridula Verhoeff, 1925: 23. *Nov. syn.*

Material examined

Syntypes. SMNH, ♀, Atherton, ♀, ♂, Cedar Creek (Ravenshoe).

Other material

QUEENSLAND: Holotype of *Parascutigera viridula*, SMNH, ♀, Atherton; syntypes of *P. mjoebergi*, SMNH, 3 ♀♀, ♂, Herberton, ♀, NHM, unspecified Queensland locality [not cited by Verhoeff (1925) but labelled "Verhoeff Collection" in Verhoeff's hand); syntypes of *P. noduligera*, SMNH, ♀, Cedar Creek (Ravenshoe), ♀, ♂, Malanda; holotype of *P. spinulata*, SMNH, ♂, Atherton; holotype of *P. viridula*, SMNH, ♀, Atherton; QM S38746, ♀, 4♂♂, S38751, ♀, S83810, ♀, Hahn Tableland (North End), 16°49′S 145°11′E, 1000 m, G.B. Monteith, D.J. Cook, G. Thompson, 13.xii.1995, rainforest; QM S38757, 2♀♀, Stone Creek, 17°18′S 146°01′E, G.B. Monteith, 7.xii.1995; QM S83798, ♂, Stone Creek, J. Hasenpusch, 2001, rainforest; QM S38986, ♀, Mt Lewis, 16 km from Bushy Ck, 16°34′S 145°16′E,

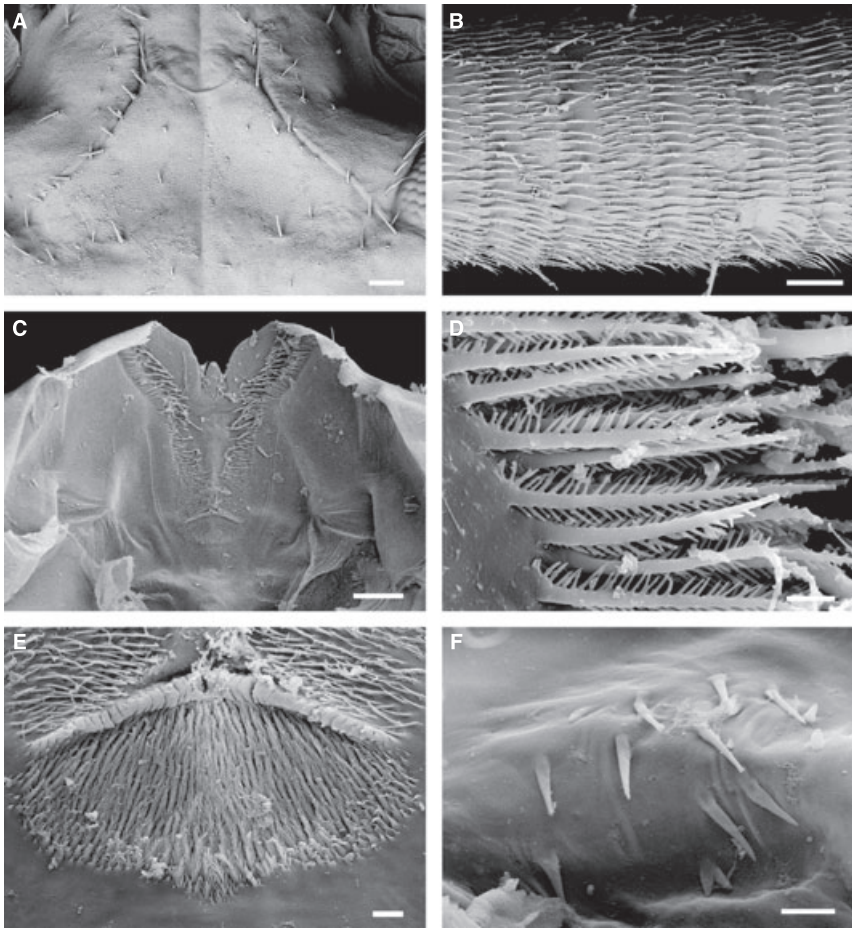

Fig. 6. *Parascutigera guttata* (Verhoeff, 1925). (A) QM S46151, male. (B–F) QM S83799, female. (A) head sutures, scale 100 μm. (B) six articles from first flagellum of antenna, scale 50 μm. (C–F) epipharynx: (C) scale 100 μm; (D) labral bristles, scale 50 μm; (E) field of branching spines on medial clypeal part of epipharynx, scale 10 μm; (F) spine cluster on lateral clypeal part of epipharynx, scale 10 μm.

900 m, G.B. Monteith, 20.iv.1997; QM S46151, ♂, Cape Upstart, 2.5 km SE of Station Hill, 19°47′S 147°49′E, 50 m, G.B. Monteith, 20.iv.1998, open forest; QM S83799, ♀, 1.5 km NW of Cape Tribulation, 0 m, G.B. Monteith, D. Yeates, G. Thompson, 8.x.1982; QM S83800, 2♀♀, 3♂♂, Hahn Tableland Radar Stn, 16°55′S 145°15′E, 950 m, G.B. Monteith, 26–27.xi.1998, open forest; QM S83801, Devil's Thumb, 12 km NW Mossman, 1000 m, 27.xii.1989, ANZSES; QM S83802, ♂, Lambs Head, 10 km W Edmonton, 1200 m, G.B. Monteith, G. Thompson, H. Janetzki, 10–12.xii.1989; QM S83803, ♀, Bellenden–Ker Range, 0.5 km S Cable Tower 7, 500 m, 1981, EARTHWATCH/Queensland Museum; QM S83804, ♀, Bellenden–Ker Range, Cable Tower 3, 1054 m, 17–24.x.1981, EARTHWATCH/Queensland Museum; QM S83805, ♂, Mt Misery via Helenvale, 750 m, Sheridan, Roberts, 6.xii.1990; QM S83806, ♀, Bakers Blue Mt, 17 km W Mt Molloy, 800–1000 m, 30.xii.1989–9.i.1990, ANZSES; QM S83807, ♂, McDowall Range, 17 km N Daintree, 520 m, G.B. Monteith, D.J. Cook, 27.xi.1985, rainforest; QM S83808, ♀, Hinchinbrook Island, Gayundah Creek, 10 m, V. Davies, J. Gallon, 7–14.xi.1984; QM S83809, ♂, Mt Halifax, 19°07′S 145°23′E, 950 m, D.J. Cook, 10.v.1991, rainforest; MCZ DNA102317, ♂, Rose Gums Wilderness Retreat, Atherton Plateau, 17°18′51.1″S 145°42′08.6″E, 770 m, G. Hormiga, L. Lopardo, 15–16.iii.2006, rainforest.

Diagnosis

Parascutigera with grey median and lateral longitudinal bands on tergal plates, dark grey to blackish patch of pigment at posterolateral corner of plates. Paired spines at base of *Stachelborsten* up to half length of bristle on TT6–7, about one-fifth length of bristles on TT2. Spicula short, conical, separated by several polygonal scales that lack spicula; spicula sparse on TT1–2. Margins of anterior tergal plates fringed by single short spines paired with a much longer *Stachelborste*; margins of TT5–7 with unpaired spines variably as long as associated *Stachelborste*. Syntelopodite of female gonopod parallel-sided to gently divergent; sinus between inner margins of mesarthron usually moderately wide, width of mesarthron averaging two-thirds maximum width of sinus.

Description

Length up to 24 mm in females, 23 mm in males.

Tergal plates pigmented by paired median longitudinal bands (separated by narrow yellow strip) of light to medium grey (Fig. 2); lateral part of tergal plates mottled light brown on yellowish background, almost always with narrow, irregular, light to dark grey

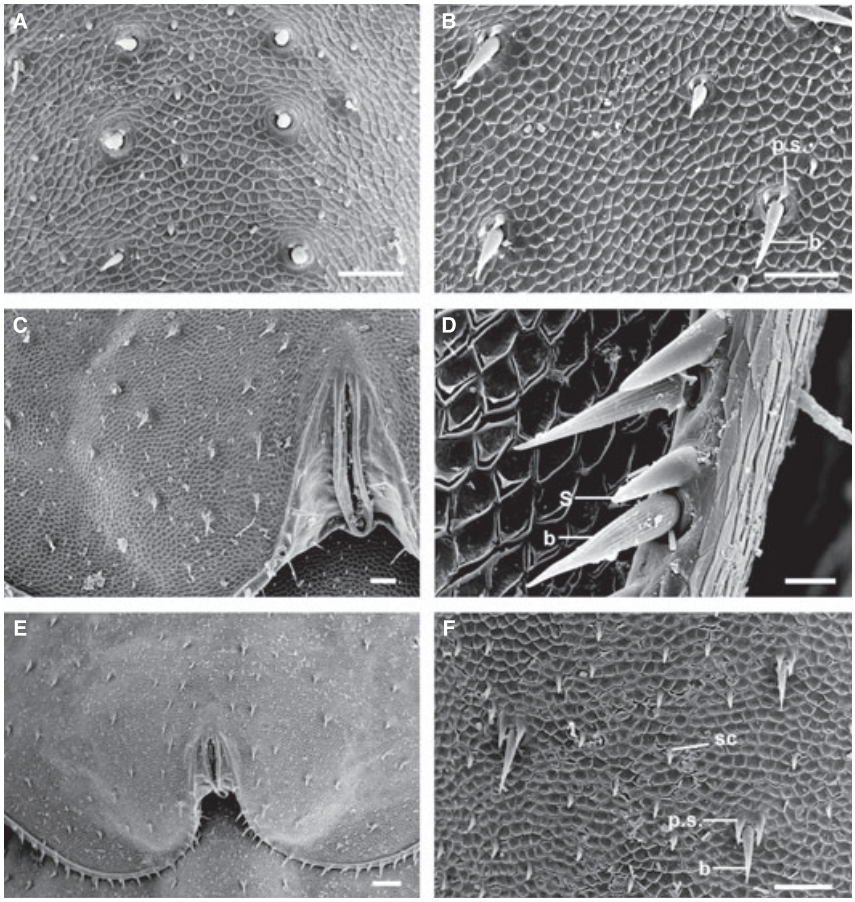

Fig. 7. *Parascutigera guttata* (Verhoeff, 1925). (A) QM S46151, male. (B–F) QM S83799, female. (A) Anteromedial part of T1, scale 50 μm. (B) Anterolateral part of T2, bristles (b) with paired spines (p.s.) at right are in medial rows, scale 50 μm. (C) Spiracle and stoma saddle on T3, scale 50 μm. (D) Spines (S) and bristles (b) on posterolateral margin of T4, scale 10 μm. (E) Stoma saddles on T6, scale 100 μm. (F) Medial part of T7, with paired spines (p.s.) at base of bristle (b), spicula (sc), scale 50 μm.

longitudinal band or longitudinally aligned series of pigment patches when discontinuous; red pigment variably present in grey longitudinal band; dark grey or almost black patch of pigment at posterolateral corner of tergal plates. Behind sutures, head pigmentation typically a V-shaped posterior patch, strip along median furrow, and variably present pair of lateral patches; pigmentation stronger in front of sutures, with purple-black to red-brown band along antennal base that extends inwards to join a median strip. Stoma saddles variably cream-coloured, pink or pale brown.

Anterior projection of head sutures short, triangular, pointed distally, slightly divergent anteriorly (Fig. 6A). First flagellum of antenna with 61–105, overwhelmingly 70–85 articles, mean 78 ($N = 32$, specimens >16 mm body length); asymmetry between numbers of articles in first flagellum on each side of a specimen usually less than ten articles, ranging to 23. Articles with two or three whorls of densely arranged, flattened, gently curved hairs, few trichoid setae in a single whorl at distal end of article (Fig. 6B).

Epipharynx typical of Scutigeridae with respect to lateral bar of labral trapezoid bearing narrow longitudinal groove along whole length of bar (Fig. 6C), labral bristles differentiated into narrow outer band of short, pectinate bristles and wider inner band of longer simple bristles (Fig. 6D). Two clusters of sensilla along midline of labral trapezoid: more distal unpaired, transverse group of about 24 bottle-shaped sensilla at termination of median ridge, and proximal cluster composed of three aggregations of sensilla at proximal sclerotized bulge; proximal aggregations comprise a lateral pair of groups of mostly bottle-shaped sensilla and a few button-shaped sensilla, and slightly distal to the lateral aggregations a median side-by-side pair of button-shaped sensilla. Median field of pectinate spines (Fig. 6E) rhomboid, lacking a subparallel-sided proximal extension seen in most scutigeromorphs. Broadly ovate cluster of about 14 nipple-shaped sensilla on medial part of clypeal triangle, a short distance behind dense field of branching spines. Lateral clusters of spines (Fig. 6F) within clypeal part of epipharynx composed of uniformly slender, elongate spines.

Outlines of tergal plates as shown in Fig. 2; most apparent variability involves relative length and width of plates (e.g. maximum width of T4 74–85% its length between rear edge of anterior border and posterior edge of spiracle) and shape of T6, with lateral margins parallel sided or distinctly converging backwards. Most specimens with all bristles developed as *Stachelborsten*; median pair of rows of bristles and most bristles on stoma saddles consistently developed as *Stachelborsten*; *Tastborsten*, when present, concentrated on lateral parts of tergal plates. Number of bristles on stoma saddles relatively consistent along trunk, mostly 9–16 on each saddle (Fig. 7C) exceptionally as few as six. Paired spines at base of *Stachelborsten* mostly about half length of bristle on TT6–7 (Fig. 7F) becoming progressively shorter on more anterior tergal plates to be about one-fifth length of bristles on TT2

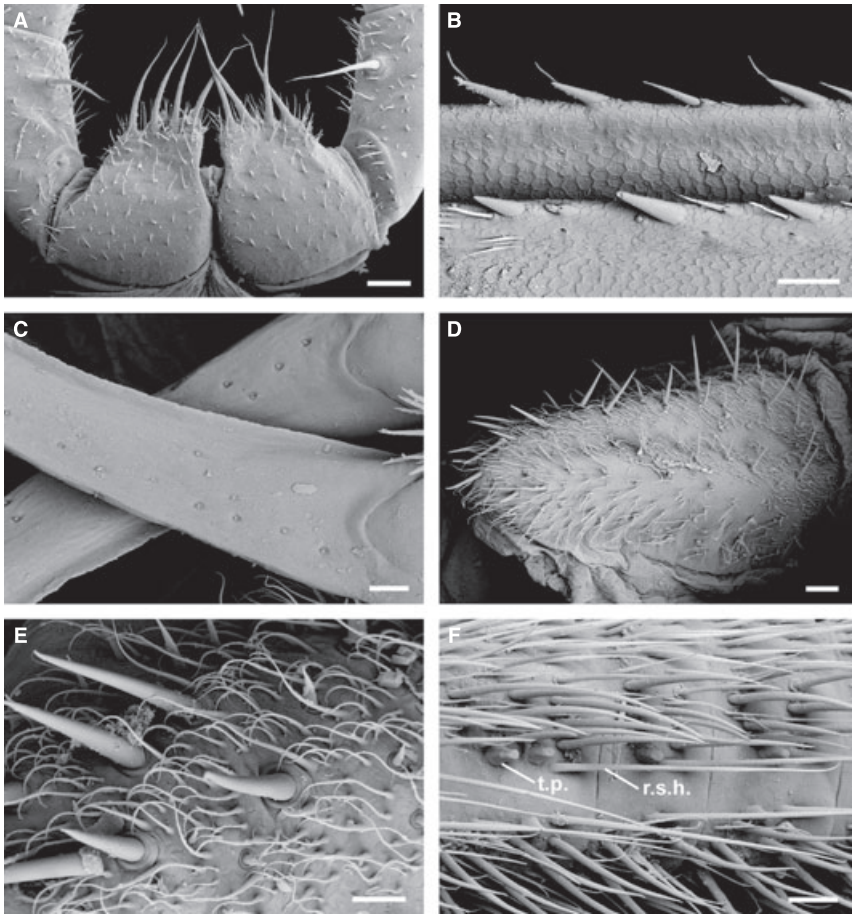

Fig. 8. *Parascutigera guttata* (Verhoeff, 1925). (A, C–E) QM S83799, female. (B) QM S46151, male. (F) QM S38986, female. (A) Maxillipede coxae, scale 200 μm. (B) Carinae on ventral side of tibia of leg 10, scale 50 μm. (C) Ventral side of metarthron of female gonopod, with row of sensilla coeloconica, scale 20 μm. (D) Subanal plate, scale 50 μm. (E) Setae and hairs on dorsodistal edge of subanal plate, scale 20 μm. (F) Ventral side of tarsus II of leg 14, showing tarsal papillae (t.p.), resilient sole hairs (r.s.h.), scale 20 μm.

(Fig. 7B); short, triangular spines on T1 (Fig. 7A). Spicula short, tapering, mostly about half length of paired spines at bristle bases on TT6–7, even where densest separated by several polygonal scales that lack spicula at their margins. Margins of TT5–7 having mostly *Stachelborsten* associated with an unpaired spine, rarely paired spines, spine generally shorter than *Stachelborste* but variably as long. Stoma saddles gently inflated (Fig. 7E).

Tarsal papillae as usual for genus, pair (exceptionally two pairs: Fig. 8F) on each tarsomere of legs 1–14, with a resilient sole hair emerging behind inner edge of each tarsal papilla. Cluster of setae on ventrolateral side of tarsus II arranged in two, or less commonly three, transverse bands of two or three (exceptionally four) setae on each side of tarsal papillae. Tarsomere numbers as follow (range in tarsus I/tarsus II): leg 1, 13–15/32–36; leg 2, 11–13/31–34; leg 3, 10–13/27–33; leg 4, 8–11/22–32; leg 5, 8–12/21–29; leg 6, 7–12/19–31; leg 7, 7–9/27–29; leg 8, 7–8/25–28; leg 9, 7–9/24–29; leg 10, 7–9/26–30; leg 11, 7–9/28–30; leg 12, 8–9/29–33; leg 13, 9–11/30–34; leg 14, 9–11/29–36.

Gonopod proportions based on 15 females of body length 16–24 mm (including types of *P. guttata*, *P. mjoebergi*, *P. noduligera*, and *P. viridula*): maximum length of gonopod 1.65–2.9 times maximum width (ratio A/B of Würmli, 1973b; fig. 1), mean 2.28; proarthron 0.9–1.7 times length of mesarthron (ratio C/D of Würmli, 1973b), mean 1.14; width of mesarthron 0.44–1.64 times maximum width of sinus (ratio F/G of Würmli, 1973b), mean 0.81; proarthron + mesarthron 1.21–2.54 times length of metarthron (ratio C + D/E of Würmli, 1973b), mean 1.82. Sinus generally parabolic in larger specimens, with bluntly pointed apex. Sensilla coeloconica on ventral face of metarthron mostly arranged in a single row (Fig. 8C). Subanal plate of female drop-shaped, maximum height slightly more than half its length, with blunt, rounded distal end and nearly symmetrical dorsal and ventral margins (Fig. 8D); smooth, sparsely setose band along middle of subanal plate along most of its length; setae on medial outer surface of subanal plate slender, those near dorsal and posterior margins thickened but not markedly spiniform; slender, curved hairs (Fig. 8E) densely arranged between setae.

Discussion

The revised diagnosis above is intended to distinguish *Parascutigera guttata* from congeners in New Caledonia and Western Australia and undescribed species from Queensland (Fig. 3D–F). The relative sparseness of the tergal spicula, where even the densest distribution on TT6 and 7 involves separation of spicula by several scales devoid of spicula (Fig. 7E, F), provides a striking difference from New Caledo-

nian species, in which nearly all tergal scales are associated with spicula (Edgecombe and Giribet, 2006; Fig. 3D for *P. latericia*; Edgecombe, 2007; fig. 2B for *P. festiva*). Detailed descriptions of well sampled scutigerid species (Edgecombe and Barrow, 2007) have reiterated the limited diagnostic value of many meristic characters laboriously tabulated by Verhoeff and employed in his taxonomy of Queensland *Parascutigera* (e.g. spine numbers on the prefemur, tibia and tarsus I of particular legs; numbers of bristles on individual stoma saddles) but critiqued by his contemporaries for showing variability on scale unappreciated by Verhoeff (Muralevič, 1910; Chamberlin, 1920).

Synonymy is most straightforward for *Parascutigera aculeata* and *P. spinulata*, each based on a single male, and for which Verhoeff raised the question of the former being a growth stage of the latter. Their distinction was based on the absence (*P. aculeata*) or presence (*P. spinulata*) of spines associated with the *Stachelborsten* on the margins of the tergal plates, a character that develops ontogenetically. Likewise *P. mjoebergi* and *P. noduligera* were distinguished based on minor differences in relative lengths of the sections of the female gonopod, noted above to intergrade, as well as trivial differences in numbers of leg spines drawn from a small sample size. The supposed species pair *P. mjoebergi* and *P. noduligera* were distinguishd in Verhoeff's key from *P. viridula* (a single specimen) based on whether or not the mesarthron is parallel-sided or divergent and the sinus between the mesarthron inner margins is triangular or more or less elliptical. As observed above (and see Fig. 3), both of these characters vary across the larger sample now available without discrete differences and, indeed, in the context of observed variation the slight divergence of the mesarthron in the holotype of *P. viridula* is a trivial difference from the types of the other putative species. The specimens used by Verhoeff to establish his six nominal species conform to pigmentation as depicted in Fig. 2, and share details of tergal prominences as depicted in Fig. 7 (spicula shapes and density, relative spine/bristle size on particular tergal plates).

The fundamental split in Verhoeff's key to his six nominal species was between putative species that have the prefemur, femur and tibia of legs 1–8 with dark flecks or rings (*P. guttata*, *P. aculeata*, *P. spinulata*) and those that allegedly either lack these flecks or rings or show at most pale traces of them on the tibia (*P. viridula*, *P. mjoebergi*, *P. noduligera*). This distinction is invalid, even using Verhoeff's type material. Syntypes of *P. noduligera* (which lacks rings according to its placement in the key) in fact have substantially more strongly ringed legs than does the holotype of *P. aculeata*. New collections demonstrate that the strength of rings varies continuously from weak to strong, even in specimens from the same collection site.

Verhoeff's key separated *P. guttata* from *P. aculeata* and *P. spinulata* based on the former having dark cherry red stoma saddles and the latter two having whitish stoma saddles. The difference in colour is not pronounced on the preserved type specimens, although it is possible that the once "dark cherry red" stoma saddles have faded in alcohol, given that some live specimens are definitely observed to have bright red stoma saddles (e.g. DNA102317). New collections from the Wet Tropics exhibit considerable variation in colour of the stoma saddles, from whitish to pink to brown, even within single populations, and the amount of red or pink pigment can vary along the length of the body. Based on these observations, colour of stoma saddles should be used as a taxonomic character with considerable caution.