Evolutionary relationships among American mud crabs (Crustacea: Decapoda: Brachyura: Xanthoidea) inferred from nuclear and mitochondrial markers, with comments on adult morphology

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Members of the brachyuran crab superfamily Xanthoidea *sensu* Ng, Guinot & Davie (2008) are a morphologically and ecologically diverse assemblage encompassing more than 780 nominal species. On the basis of morphology, Xanthoidea is presently regarded to represent three families: Xanthidae, Pseudorhombilidae, and Panopeidae. However, few studies have examined this superfamily using modern phylogenetic methods, despite the ecological and economic importance of this large, poorly understood group. In this study we examine phylogenetic relationships within the superfamily Xanthoidea using three mitochondrial markers, *12S* rRNA, *16S* rRNA, and *cytochrome oxidase I* (COI), and three nuclear markers, *18S* rRNA, *enolase* (ENO) and *histone H3* (H3). Bayesian and maximum-likelihood analyses indicate that the superfamily Xanthoidea is monophyletic; however, the families Xanthidae, Panopeidae, and Pseudorhombilidae, as defined by Ng *et al.*, are not, and their representative memberships must be redefined. To this end, some relevant morphological characters are discussed.

INTRODUCTION

Commonly known as mud, pebble, rubble, or black-fingered crabs (Davie, 2002: 505), members of the superfamily Xanthoidea MacLeay, 1838 (*sensu* Ng *et al.*, 2008) are familiar forms in many marine settings, but many xanthoid taxa remain poorly described and lack detailed illustrations. As a result, xanthoids encountered in environmental studies are often misidentified or referred to simply as 'unidentified xanthids' (Overstreet & Heard, 1978; Boschi, 1979; Poupin, 2003; Hewitt, 2004). This appears to be

due to, at least in part, a high degree of morphological convergence among representatives of the group and inadequate diagnoses of xanthoid taxa from species to family level (e.g. Guinot, 1967, 1969a–c, 1978; Schubart, Neigel & Felder, 2000; Felder & Martin, 2003; Ng *et al.*, 2008; Thoma, Schubart & Felder, 2009; Felder & Thoma, 2010; Lai *et al.*, 2011; Thoma & Felder, 2012; Lasley, Lai & Thoma, 2013).

Representatives of the superfamily Xanthoidea are found worldwide in shallow temperate and tropical waters of intertidal to continental slope habitats. While the family Xanthidae MacLeay, 1838 is circumtropical, the families Panopeidae Ortmann, 1893, and Pseudorhombilidae Alcock, 1900 are known almost exclusively from waters of the Americas.

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Although several species of Panopeidae have been introduced in both the eastern Atlantic [e.g. *Dyspanopeus sayi* (Smith, 1869), *Rhithropanopeus harrisii* (Gould, 1841)] and the western Pacific [e.g. *Acantholobulus pacificus* (Edmondson, 1931) and *Panopeus lacustris* Desbonne, in Desbonne & Schramm, 1867)], only *Panopeus africanus* A. Milne-Edwards, 1867 and *Eurypanopeus blanchardi* (A. Milne-Edwards, 1880) (see Milne-Edwards, 1873–1880) are known to occur naturally outside of the Americas (e.g. Edmondson, 1931, 1962; Naylor, 1960; Manning & Holthuis, 1981; Froglia & Speranza, 1993; Galil, Froglia & Noël, 2002; Felder & Martin, 2003; Carlton & Eldredge, 2009; Petrescu *et al.*, 2010; Ahyong & Wilkens, 2011; Brockerhoff & McLay, 2011; Castro, 2011).

As part of ongoing investigations of brachyuran evolution, we have undertaken a re-examination of the phylogenetic relationships among those species from coasts of the Americas that are currently assigned to the superfamily Xanthoidea. While the present study focuses on the families Panopeidae and Pseudorhombilidae, it builds upon previous efforts (Thoma *et al.*, 2009) to clarify species composition of the xanthoid families and determine relationships between the three families (i.e. Panopeidae, Pseudorhombilidae, and Xanthidae).

The present work serves as a companion to recent work by Lai *et al.* (2011), focused on the family Xanthidae, by treating the families Panopeidae and Pseudorhombilidae. In addition, the present analysis utilizes fragments of three mitochondrial genes [i.e. *12S* rRNA; *16S* rRNA; *cytochrome oxidase I* (COI)] and three nuclear genes [i.e. *enolase* (ENO); *histone H3* (H3); *18S* rRNA] to provide a framework for future revisionary works.

MATERIALS AND METHODS
TAXON SELECTION
Sequences from 234 individuals representing 114 nominal species were initially analysed to ensure accuracy and quality of the data. Duplicate taxa and any inconsistent sequences were removed from subsequent analyses, which resulted in a final dataset of 113 individuals representing 111 nominal species, 57 nominal genera, and three families (excluding outgroup taxa; Table 1). Although the composition of Xanthoidea has often been debated, several recent phylogenetic analyses support a monophyletic Xanthoidea *sensu* Ng *et al.* (2008) (Thoma *et al.*, 2009; Lai *et al.*, 2011, 2014; Lasley *et al.*, 2013). These reports, and other unpublished analyses, support the present selection of outgroup taxa including *Eriphia gonagra* (Fabricius, 1781), *Lobopilumnus agassizii* Stimpson, 1871 (Stimpson, 1871b), *Menippe*

mercenaria (Say, 1817–1818), and *Acidops fimbriatus* Stimpson, 1871 (Stimpson, 1871a), as these taxa have been shown to be related to but outside of Xanthoidea *sensu* Ng *et al.* (2008).

Specimens used in this study were collected primarily during recent research cruises and field expeditions. Specimens were either directly preserved in 80% ethyl alcohol (EtOH) or frozen in seawater or glycerol at −80 °C before transfer to 80% EtOH and subsequent archival in the University of Louisiana at Lafayette Zoological Collections, Lafayette, LA, USA (ULLZ). Additional similarly preserved materials were obtained on loan from the Florida Museum of Natural History, University of Florida, Gainesville, FL, USA (FLMNH). When possible, identification of specimens was confirmed by two or more investigators to limit the risk of misidentifications. Additional abbreviations used throughout include: G1, first male pleopod or first gonopod; P5, fifth pereopod. The somites of the thoracic sternum and sternites are numbered from 1 to 8, so that the last two sternites are termed sternites 7 and 8.

COLLECTION OF GENETIC DATA
Genomic DNA was extracted from muscle tissue of pereopods for representatives of the superfamily Xanthoidea, using a Qiagen DNeasy Blood and Tissue Kit (Qiagen) following the manufacturer's protocol. Using polymerase chain reaction (PCR), fragments of the following three mitochondrial and three nuclear markers were amplified; approximately 550 bp of 16S rRNA using the primers 1472 or 16Sbr in combination with 16 L2 and 16Sar; approximately 345 bp of 12S rRNA using 12sf and 12s1r; approximately 600–650 bp of COI using LCO-1490 and HCO-2198 or Pano-F and Pano-R; approximately 325 bp of H3 using Hex-AF and Hex-AR; approximately 600 bp of 18S rRNA using 18S-O and 18S-B; and approximately 395 bp of ENO using EnolA and EnolS (see Table 2 for complete primer information). Each PCR was performed in 25-μL volumes containing: 0.4 μM of each primer, 200 μM of each dNTP, 2.5 μL 10× PCR buffer, 2 mM MgCl$_2$, 1 unit Fermentas DreamTaq Green DNA Polymerase (Thermo Fisher Scientific), and 30–50 ng of genomic DNA. Reactions were carried out using the following cycling parameters: initial denaturation at 94 °C for 2 min; 35 cycles at 94 °C for 25 s, 48 °C (16S), 60 °C (12S), 58 °C (18S), 52 °C (COI), 50 °C (ENO), or 66 °C (H3) for 1 min, and 72 °C for 1 min; and a final extension at 72 °C for 10 min. PCR products were purified using an EPOCH GenCatch PCR Clean-up Kit (EPOCH BioLabs) and sequenced in both directions using an ABI BigDye Terminator v3.1 Cycle Sequencing Kit (Life Technologies). Cycle sequencing products were purified using

Table 1. Crab species used for phylogeny reconstruction, showing catalogue number, collection locality, and GenBank accession numbers for partial sequences of 12S, 16S, 18S, cytochrome C oxidase subunit I (COI), enolase (ENO), and Histone-3 (H3)

Taxon	Locality	GenBank accession numbers					
		12S	16S	18S	COI	ENO	H3
Xanthidae							
Actaea acantha (H. Milne Edwards, 1834) – ULLZ 9966	Belize, Carrie Bow Cay	KF683046	KF682996	–	KF682768	KF682650	KF682542
Actaea bifrons Rathbun, 1898 – ULLZ 7843	USA, Gulf of Mexico, off St. Petersburg, Florida	GU144430	GU144458	KF682859	KF682803	KF682629	GU144487
Allactaea lithostrota Williams, 1974 – ULLZ 4613	USA, Gulf of Mexico, off Louisiana	GU144428	GU144456	KF682848	JQ277192	KF682651	GU144485
Banareia palmeri (Rathbun, 1894) – ULLZ 8187	USA, Gulf of Mexico, off Alabama	KF683042	KF683003	KF682841	KF682814	KF682652	KF682544
Carpoporus papulosus Stimpson, 1871 – ULLZ 7355	México, Gulf of Mexico, off Merida	GU144429	GU144457	KF682878	JQ277193	KF682627	GU144486
Cataleptodius floridanus (Gibbes, 1850) – ULLZ 4806	USA, Florida, Ft. Pierce	GU144422	GU144449	KF682875	KF682740	KF682645	GU144478
Cataleptodius occidentalis (Stimpson, 1871) – ULLZ 4127	México, Baja California Sur, Puerto San Carlos	KF683026	–	KF682876	KF682828	KF682655	KF682591
Chlorodiella longimana (H. Milne Edwards, 1834) – ULLZ 12144	Panama, off Bocas del Toro	JQ277169	JQ277177	KF682877	JQ277196	KF682633	JQ277204
Cyclodius obscurus (Hombron & Jacquinot, 1846) – ULLZ 9034	USA, Hawaii, Oahu Island	GU144431	GU144459	KF682844	JQ277194	KF682641	GU144488
Edwardsium lobipes (Rathbun, 1898) – ULLZ 9321	Panama, Pearl Islands	GU144427	GU144453	KF682847	JQ277189	KF682677	GU144482
Etisus guinotae Felder & Thoma, 2010 – ULLZ 10936	USA, Gulf of Mexico, off Louisiana	KF683032	KF682948	KF682888	KF682743	KF682665	KF682582
Etisus maculatus (Stimpson, 1860) – ULLZ 10008	Belize, Carrie Bow Cay	KF683043	KF683008	KF682886	KF682739	KF682654	KF682549
Eucratodes agassizii A. Milne-Edwards, 1880 – ULLZ 10965	USA, Gulf of Mexico, off Louisiana	KF683023	KF682951	KF682922	KF682808	KF682643	KF682581
Garthiope barbadensis (Rathbun, 1921) – ULLZ 11173	Belize, Carrie Bow Cay	KF683048	KF682988	KF682892	KF682748	KF682728	KF682571
Garthiope spinipes (A. Milne-Edwards, 1880) – ULLZ 7840	USA, Gulf of Mexico, off St. Petersburg, Florida	GU144410	GU144438	KF682936	KF682750	KF682676	GU144494
Glyptoxanthus erosus (Stimpson, 1859) – ULLZ 10634	USA, Gulf of Mexico, off Louisiana	KF683024	KF682956	KF682866	KF682737	KF682712	KF682599
Glyptoxanthus labyrinthicus (Stimpson, 1860) – ULLZ 11361	Panama, Pearl Islands	KF683027	KF682972	KF682840	KF682742	KF682692	KF682596
Glyptoxanthus vermiculatus (Lamarck, 1818) – ULLZ 7865	USA, Gulf of Mexico, off St. Petersburg, Florida	KF683055	KF683007	KF682867	–	KF682717	KF682545
Heteractaea lunata (Lucas, in H. Milne Edwards & Lucas, 1844) – ULLZ 12316	Panama, Pearl Islands	KF683011	KF682966	KF682851	KF682801	–	KF682589
Medaeops granulosus (Haswell, 1882) – ULLZ 6500	USA, Hawaii, Oahu Island	GU144419	GU144447	KF682873	KF682805	KF682664	GU144473
Melybia thalamita Stimpson, 1871 – ULLZ 7870	USA, Gulf of Mexico, off Louisiana	KF683014	KF682945	KF682881	KF682786	KF682689	KF682537
Microcassiope taboguillensis (Rathbun, 1907) – ULLZ 11881	Panama, Cohiba Island	KF683035	KF682967	KF682854	KF682825	KF682698	KF682573
Microcassiope xantusii (Stimpson, 1871) – ULLZ 11880	Panama, Cohiba Island	KF683036	KF683006	KF682853	KF682827	KF682699	KF682546
Micropanope lobifrons A. Milne-Edwards, 1881 – ULLZ 6678	USA, Gulf of Mexico, off Louisiana	GU144412	GU144439	KF682906	KF682818	KF682622	GU144504
Micropanope pusilla A. Milne-Edwards, 1880 – ULLZ 6776	México, Gulf of Mexico, off Merida	KF683050	KF682991	KF682887	KF682795	KF682634	KF682556
Micropanope sculptipes Stimpson, 1871 – ULLZ 6603	USA, Gulf of Mexico, off Dry Tortugas, Florida	EU863338	EU863404	KF682891	KF682804	KF682649	KF682552
Micropanope truncatifrons Rathbun, 1898 – ULLZ 7359	USA, Gulf of Mexico, off Louisiana	GU144406	GU144434	KF682934	KF682809	KF682661	GU144490
Neoliomera pubescens (H. Milne Edwards, 1834) – FLMNH 8779	USA, Hawaii, Oahu Island	KF683037	KF682992	KF682868	KF682830	KF682632	KF682543
Paractaea rufopunctata (H. Milne Edwards, 1834) – ULLZ 8946	Panama, off Bocas del Toro	GU144415	GU144442	KF682849	KF682766	KF682682	GU144472
Paraxanthias taylori (Stimpson, 1861) – ULLZ 5875	USA, California	JQ277168	JQ277179	KF682850	JQ277198	KF682715	JQ277203
Paraxanthus barbiger (Poeppig, 1836) – ULLZ 11409	Chile, Valdivia	KF683038	KF682997	KF682885	KF682769	KF682647	KF682550
Pilodius areolatus (H. Milne Edwards, 1834) – ULLZ 9033	USA, Hawaii, Oahu Island	GU144420	GU144448	KF682843	JQ277191	KF682709	GU144474
Platyactaea dovii Stimpson, 1871 – ULLZ 9043	Panama, Pearl Islands	GU144424	GU144451	KF682869	KF682822	KF682705	GU144480
Platyactaea setigera (H. Milne Edwards, 1834) – ULLZ 11178	Belize, Carrie Bow Cay	KF683053	KF682980	KF682842	KF682821	KF682625	KF682541
Platypodiella spectabilis (Herbst, 1794) (see Herbst, 1782–1804) – ULLZ 11077	Belize, Carrie Bow Cay	KF683041	KF682989	KF682839	KF682810	KF682624	KF682558
Pseudomedaeus agassizii (A. Milne-Edwards, 1880) – ULLZ 9018	USA, Florida, Ft. Pierce	KF683047	KF682995	KF682846	KF682802	KF682725	KF682539
Pseudomedaeus distinctus (Rathbun, 1898) – ULLZ 10402	USA, off Louisiana	KF683013	KF682962	KF682845	KF682731	KF682691	KF682590
Scolopius nuttingii (Rathbun, 1898) – ULLZ 6732	México, Gulf of Mexico, off Merida	KF683045	KF682990	KF682927	KF682788	KF682713	KF682559

Taxon	Locality						
Speocarcinus carolinensis Stimpson, 1859 – ULLZ 12372	USA, Florida, Ft. Pierce	KF683031	KF682947	KF682931	KF682807	KF682724	KF682585
Speocarcinus granulimanus Rathbun, 1894 – ULLZ 12781	Costa Rica, off Puerto Viejo	KF683057	KF682982	KF682897	KF682745	KF682653	KF682610
Speocarcinus lobatus Guinot, 1969 – ULLZ 11957	USA, Gulf of Mexico, off Louisiana	KF683021	KF682974	KF682907	KF682751	KF682660	KF682601
Speocarcinus meloi D'Incao & Gomes da Silva, 1992 – ULLZ 12373	Panama, off Bocas del Toro	KF683018	KF682973	KF682860	KF682744	KF682658	KF682602
Speocarcinus monotuberculatus Felder & Rabalais, 1986 – ULLZ 7562	México, Gulf of Mexico, off Campeche	EU863293	EU863359	KF682941	KF682819	KF682697	GU144497
Williamstimpsonia denticulatus (White, 1848) – ULLZ 6451	Belize, Twin Cays	KF683044	KF683004	KF682942	KF682738	KF682711	KF682572
Xanthodius stimpsoni (A. Milne-Edwards, 1879) – ULLZ 12005	Panama, Pearl Islands	KF683029	KF682971	KF682879	KF682770	KF682694	KF682600
Xanthodius americanus (Saussure, 1858) – ULLZ 7031	México, Gulf of Mexico, off Campeche	JQ277167	JQ277178	KF682870	JQ277199	KF682630	JQ277207
Xanthodius cooksoni (Miers, 1877) – ULLZ 5849	Nicaragua, Estero Nagualapa	KF683040	KF683002	KF682884	KF682741	KF682666	KF682557
Panopeidae							
Acantholobulus bermudensis (Benedict & Rathbun, 1891) – ULLZ 6924	USA, Florida, Ft. Pierce	EU863306	EU863372	KF682871	KF682779	KF682686	GU144464
Acantholobulus caribbeaus (Stimpson, 1871) – ULLZ 7743	USA, Florida, Ft. Pierce	EU863287	EU863353	KF682874	KF682812	KF682696	KF682604
Acantholobulus sp. nov. – ULLZ 12801	Nicaragua, Puerto Sandino	KF683059	KF682950	KF682863	KF682798	KF682680	KF682616
Acantholobulus sp. nov. nr. *A. schmitti* – ULLZ 12112	Belize, Dangriga	KF683017	KF682970	KF682865	KF682787	KF682727	BT102708
Acantholobulus pacificus (Edmondson, 1931) – ULLZ 12959	USA, Hawaii	KF683025	KF682977	KF682872	KF682778	KF682688	KF682536
Acantholobulus schmitti (Rathbun, 1930) – ULLZ 6613	Brazil, São Paulo	EU863298	EU863364	–	KF682783	KF682619	KF682564
Chasmophora macrophthalma (Rathbun, 1898) – ULLZ 11995	Panama, Panama Bay	KF683033	KF682998	KF682905	KF682747	KF682703	KF682574
Cyrtoplax panamensis Ziesenhenne in Garth, 1940 – ULLZ 12771	Costa Rica, Gulf of Nicoya	KF683039	KF682987	KF682917	KF682815	KF682681	KF682608
Cyrtoplax spinidentata (Benedict, 1892) – ULLZ 8423	USA, Florida, Ft. Pierce	EU863303	EU863369	KF682903	KF682759	KF682626	GU144501
Dyspanopeus sayi (Smith, 1869) – ULLZ 7227	USA, Florida, Ft. Pierce	EU863329	EU863395	KF682928	KF682790	KF682678	KF682579
Dyspanopeus texanus (Stimpson, 1859) – ULLZ 4039	México, Yucatán, Río Lagartos	KF683060	KF682999	KF682939	KF682791	KF682707	KF682538
Eucratopsis crassimanus (Dana, 1851) – ULLZ 6427	USA, Florida, Ft. Pierce	EU863326	EU863392	KF682837	KF682799	KF682640	KF682576
Eurypanopeus abbreviatus (Stimpson, 1860) – ULLZ 3753	USA, Florida, Ft. Pierce	EU863322	EU863388	KF682944	KF682823	KF682669	KF682575
Eurypanopeus ater Rathbun, 1930 – ULLZ 4019	México, Veracruz	KF683022	KF682965	KF682910	KF682824	KF682726	KF682594
Eurypanopeus depressus (Smith, 1869) – ULLZ 6077	USA, Florida, Tampa Bay	EU863324	EU863390	KF682880	KF682789	KF682723	KF682577
Eurypanopeus dissimilis (Benedict & Rathbun, 1891) – ULLZ 5878	USA, Florida, Ft. Pierce	EU863330	EU863396	KF682836	KF682792	KF682623	KF682578
Eurypanopeus ovatus (Benedict & Rathbun, 1891) – ULLZ 9041	México, Baja California Sur, Bahía Concepción	KF683019	KF682960	KF682909	KF682733	KF682671	KF682586
Eurypanopeus planissimus (Stimpson, 1860) – ULLZ 4140	México, Baja California Sur, Bahía Concepción	EU863320	EU863386	BT088402	KF682765	KF682621	KF682567
Eurypanopeus planus (Smith, 1869) – ULLZ 12789	Nicaragua, El Estero de Aserradores	KF683063	KF682954	KF682893	KF682760	KF682631	KF682615
Eurypanopeus turgidus (Rathbun, 1930) – ULLZ 9038	USA, Texas	KF683010	KF682964	KF682901	KF682817	KF682716	KF682597
Eurytium affine (Streets & Kingsley, 1877) – ULLZ 5499	México, Baja California Sur, Puerto San Carlos	KF683020	KF682963	KF682902	KF682757	KF682687	KF682583
Eurytium albidigitum Rathbun, 1933 – ULLZ 4156	México, Baja California Norte, Bahia de los Angeles	KF683067	KF682958	KF682918	KF682826	KF682693	KF682595
Eurytium limosum (Say, 1818) (see Say, 1817–1818) – ULLZ 4012	México, Veracruz	GU144421	GU144455	KF682838	KF682755	KF682690	GU144477
Eurytium tristani Rathbun, 1906 – ULLZ 12791	Nicaragua, Paso Caballos	KF683070	KF682953	KF682913	KF682756	KF682679	KF682612
Glyptoplax pugnax Smith, 1870 – FLMNH 3667	Panama, Panama City	KF683065	KF682946	KF682946	KF682813	KF682708	KF682547
Glyptoplax smithii A. Milne-Edwards, 1880 – ULLZ 8142	USA, Gulf of Mexico, off Cape San Blas, Florida	EU863284	EU863350	KF682937	KF682800	KF682667	KF682560
Hexapanopeus angustifrons (Benedict & Rathbun, 1891) – ULLZ 6943	USA, Florida, Capron Shoal	EU863277	EU863343	KF682894	KF682832	KF682637	KF682605
Hexapanopeus angustifrons (Benedict & Rathbun, 1891) – ULLZ 8368	USA, Florida, off St. Petersburg	EU863314	EU863380	KF682916	KF682833	KF682683	GU144465
Hexapanopeus sp. nov. – ULLZ 12779	Costa Rica, Gulf of Nicoya, off Playa Hermosa	KF683065	KF682993	KF682935	–	KF682673	KF682607
Hexapanopeus sp. nov. – ULLZ 12526	Belize, South Water Cay	KF683061	KF682952	KF682930	KF682772	KF682722	KF682613
Hexapanopeus paulensis Rathbun, 1930 – ULLZ 6608	Brazil, São Paulo	EU863307	EU863373	–	KF682831	KF682657	KF682593
Hexapanopeus paulensis Rathbun, 1930 – ULLZ 6882	USA, Gulf of Mexico, off Texas	EU863309	EU863375	KF682904	KF682829	KF682721	KF682588
Lophopanopeus bellus (Stimpson, 1860) – FLMNH 3667	USA, Washington	KF683056	KF683001	KF682929	KF682820	KF682620	KF682540
Lophoxanthus lamellipes (Stimpson, 1860) – ULLZ 9313	Panama, Coiba Island	GU144425	GU144452	KF682882	KF682782	KF682675	GU144481
Malacoplax californiensis (Lockington, 1877) – ULLZ 10572	México, Baja California Sur, Gulf of California	GU144433	GU144460	KF682923	KF682732	KF682648	GU144506
Metopocarcinus concavatus Crane, 1947 – ULLZ 12800	Nicaragua, Puerto Sandino	KF683072	KF682949	KF682864	KF682784	KF682700	KF682614

Table 1. *Continued*

Taxon	Locality	GenBank accession numbers					
		12S	16S	18S	COI	ENO	H3
Milnepanopeus lobipes (A. Milne-Edwards, 1880) – ULLZ 7828	USA, Gulf of Mexico, off Louisiana	EU863286	BT070812	KF682914	KF682816	KF682719	KF682617
Neopanope packardii (Kingsley, 1879) – ULLZ 3772	USA, Florida, Ft. Pierce	EU863283	EU863349	KF682862	KF682794	KF682706	GU144499
Gen. nov., sp. nov. near *A. schmitti* – ULLZ 8646	USA, Texas	EU863295	EU863361	–	–	KF682684	KF682563
Panopeus africanus A. Milne-Edwards, 1867 – ULLZ 4273	Spain, Cadiz	EU863304	EU863370	KF682933	KF682761	KF682729	KF682565
Panopeus americanus Saussure, 1857 – ULLZ 8456	USA, Florida, Ft. Pierce	EU863279	EU863345	KF682912	KF682774	KF682720	KF682561
Panopeus austrobesus Williams, 1983 – ULLZ 8525	Brazil, São Paulo	KF683073	KF682983	KF682921	KF682758	–	KF682569
Panopeus chilensis H. Milne Edwards & Lucas, 1843 – ULLZ 4685	Nicaragua, El Estero de Aserradores	KF683062	KF682955	KF682900	KF682771	KF682714	KF682598
Panopeus harttii Smith, 1869 – ULLZ 11986	Belize, Twin Cays	KF683016	KF682975	KF682890	KF682764	KF682674	KF682535
Panopeus herbstii H. Milne Edwards, 1834 – ULLZ 8457	USA, South Carolina	EU863296	EU863362	KF682919	KF682735	KF682638	GU144466
Panopeus lacustris Desbonne, in Desbonne & Schramm, 1867 – ULLZ 3818	USA, Florida, Ft. Pierce	EU863297	EU863363	KF682911	KF682776	KF682672	KF682548
Panopeus obesus Smith, 1869 – ULLZ 3761	USA, Florida, St. Teresa	KF683069	KF682961	KF682915	KF682775	KF682670	KF682566
Panopeus occidentalis Saussure, 1857 – ULLZ 8643	Florida, Panama City	EU863328	EU863394	KF682896	KF682763	KF682695	KF682592
Panopeus purpureus Lockington, 1877 – ULLZ 4139	México, Baja California Sur, Bahia Concepción	KF683068	KF683000	KF682938	KF682762	KF682639	KF682570
Panopeus rugosus A. Milne-Edwards, 1880 – ULLZ 8522	Brazil, São Paulo, São Vicente	KF683064	KF682969	KF682920	KF682773	KF682646	KF682580
Panopeus simpsoni Rathbun, 1930 – ULLZ 4813	USA, Florida, Ft. Pierce	KF683071	KF682994	KF682940	KF682736	KF682710	KF682562
Panoplax depressa Stimpson, 1871 – ULLZ 8056	USA, Gulf of Mexico, off St. Petersburg, Florida	EU863281	EU863347	KF682899	KF682785	KF682636	GU144493
Rhithropanopeus harrisii (Gould, 1841) – ULLZ 3995	USA, Texas	EU863280	EU863346	KF682856	KF682793	KF682668	GU144498
Robertsella mystica Guinot, 1969 – ULLZ 6469	USA, Florida, Florida Straits	KF683012	KF682957	KF682852	KF682749	KF682718	KF682606
Tetraplax quadridentata (Rathbun, 1898) – ULLZ 12374	Panama, off Bocas del Toro	KF683030	KF682959	KF682855	KF682754	KF682659	KF682584
Tetraxanthus rathbunae Chace, 1939 – FLMNH 3750	USA, Florida, off Tarpon Springs	KF683009	KF682968	KF682926	KF682806	KF682644	KF682603
Thalassoplax angusta Guinot, 1969 – ULLZ 10869	USA, Gulf of Mexico, off Louisiana	KF683052	KF682978	KF682898	KF682752	KF682628	KF682555
Pseudorhombilidae							
Chacellus filiformis Guinot, 1969 – ULLZ 12296	USA, Gulf of Mexico, off Louisiana	KF683051	KF682979	KF682889	KF682797	KF682704	KF682611
Euphrosynoplax campechiensis Vázquez-Bader & Gracia, 1991 – ULLZ 11873	USA, Louisiana	KF683049	KF682986	KF682895	KF682780	KF682701	KF682553
Euphrosynoplax sp. – ULLZ 3816	Jamaica, off Tryall	KF683015	KF682984	KF682925	KF682777	KF682642	KF682554
Nanoplax xanthiformis (A. Milne-Edwards, 1880) – ULLZ 6914	México, Gulf of Mexico, off Merida	KF683054	KF682981	KF682924	KF682796	KF682702	KF682551
Gen. nov., sp. nov. near *G. barbadensis* – ULLZ 8170	USA, Gulf of Mexico, off Alabama	EU863301	EU863367	KF682908	KF682781	KF682656	KF682587
Oediplax granulata Rathbun, 1893 – ULLZ 12386	Costa Rica, off Punta Islita	KF683367	KF682976	–	KF682746	KF682663	KF682618
Pseudorhombila quadridentata (Latreille, 1828) (see Latreille, 1825–1828) – ULLZ 9326	USA, off Texas	GU144426	GU144454	KF682835	JQ277190	KF682635	GU144483
Pseudorhombila xanthiformis Garth, 1940 – ULLZ 12778	Costa Rica, off Puerto Viejo	KF683066	KF682985	KF682857	KF682753	KF682685	KF682609
Trapezioplax tridentata (A. Milne-Edwards, 1880) – ULLZ 8054	USA, Gulf of Mexico, off Louisiana	EU863278	EU863344	KF682932	KF682811	KF682662	GU144500
Acidopsidae							
Acidops fimbriatus Stimpson, 1871 – ULLZ 9047	Panama, Pearl Islands	KF683034	KF683005	KF682883	KF682730	–	KF682568
Eriphiidae							
Eriphia gonagra (Fabricius, 1781) – ULLZ 5463	USA, Florida, Ft. Pierce	HM637933	HM637964	HM637998	HM638035	–	HM596633
Menippidae							
Menippe mercenaria (Say, 1818) (see Say, 1817–1818) – ULLZ 5464	USA, Florida, Tampa Bay	HM637944	HM637974	HM638013	HM638049	–	HM596627
Pilumnidae							
Lobopilumnus agassizii (Stimpson, 1871) – ULLZ 7121	México, Gulf of Mexico, off Merida	EU863336	EU863402	HM638010	HM638046	–	GU144475

ULLZ, University of Louisiana at Lafayette Zoological Collection, Lafayette, LA; FLMNH, Florida Museum of Natural History, University of Florida, Gainesville, FL.

Table 2. Primers used in this study

Gene	Primer	Sequence 5′→3′	Ref.
16S	16Sar	CGCCTGTTTATCAAAAACAT	(1)
16S	16Sbr	CCGGTCTGAACTCAGATCACGT	(1)
16S	16 L2	TGCCTGTTTATCAAAAACAT	(2)
16S	1472	AGATAGAAACCAACCTGG	(3)
12S	12sf	GAAACCAGGATTAGATACCC	(4)
12S	12s1r	AGCGACGGGCGATATGTAC	(4)
COI	LCO-1490	GGTCAACAAATCATAAAGATATTG	(5)
COI	HCO-2198	TAAACTTCAGGGTGACCAAAAAATCA	(5)
COI	Pano-F	GGTGCATGAGCYGGHATAGTWGG	(*)
COI	Pano-R	RTGTTGRTATARTACAGGRTCTCC	(*)
Histone-3	Hex-AF	ATGGCTCGTACCAAGCAGACGGC	(6)
Histone-3	Hex-AR	ATATCCTTGGCATGATGGTGAC	(6)
18S	18S-B	TGATCCTTCCGCAGGTTCACCT	(7)
18S	18S-O	AAGGGCACCACCAGGAGTGGAG	(8)
Enolase	EnolA	CAGCAATCAATGTCATCAAYGGWGG	(9)
Enolase	EnolA2	AGTTGGCTATGCAGGARTTYATGAT	(9)
Enolase	EnolS	ACTTGGTCAAATGGRTCYTCAAT	(9)

References: 1, Palumbi & Benzie (1991); 2, Schubart, Cuesta & Felder (2002); 3, Crandall & Fitzpatrick (1996); 4, Buhay *et al*. (2007); 5, Folmer *et al*. (1994); 6, Svenson & Whiting (2004); 7, Medlin *et al*. (1988); 8, Apakupakul, Siddall & Burreson (1999); 9, Tsang *et al*. (2011); *, present study.

Sephadex G-50 columns (Sigma-Aldrich Chemicals). Sequencing products were run on an ABI PRISM 3130*xl* Genetic Analyzer (Life Technologies) at the University of Louisiana at Lafayette.

PHYLOGENETIC ANALYSES

Sequences were assembled using Sequencher 4.9 (GeneCodes). Once assembled, sequences were aligned in MAFFT using the Q-INS-i and E-INS-I algorithms for rDNA and protein-coding DNA, respectively (Katoh *et al*., 2005; Katoh & Toh, 2008). The model of evolution that best fit each of the datasets was determined by likelihood tests as implemented in MrAIC (Nylander, 2004) under the Akaike Information Criterion (AIC). Maximum-likelihood (ML) analysis was performed in RAxML 7.2.8 (Stamatakis, 2006) and Bayesian Inference (BI) analyses of the concatenated dataset were conducted in MrBayes 3.1.2 (Huelsenbeck & Ronquist, 2001), with computations performed on the computer cluster of the Cyber-Infrastructure for Phylogenetic RESearch project (CIPRES) at the San Diego Supercomputer Center (Miller, Pfeiffer & Schwartz, 2010). A Markov Chain Monte Carlo (MCMC) algorithm with two runs of four chains each was run for 20 000 000 generations, sampling one tree every 1000 generations. A 50% majority rule consensus tree was obtained from the 20 000 trees (10 000 per run) taken after the standard deviation between runs dropped below 0.01. Clade support

was assessed with 1000 ML bootstrap replications (BS) and posterior probabilities (pP).

RESULTS

The final sequence alignments, including gaps, were 525 bp for the 16S dataset, 406 bp for 12S, 572 bp for COI, 316 bp for H3, 592 bp for 18S, and 377 bp for ENO. Likelihood tests, as implemented in MrAIC, revealed the model of DNA substitution as best fit for 16S, 12S, and 18S was HKY+I+G (Hasegawa, Kishino & Yano, 1985), GTR+I+G (Rodríguez *et al*., 1990) for COI and H3, and SYM+I+G (Zharkikh, 1994) for ENO.

Analyses of individual markers revealed largely congruent topologies. Phylogenetic relationships among 111 species of Xanthoidea *sensu* Ng *et al*. (2008) were inferred using both ML and BI approaches for the concatenated six-marker dataset. Each analysis recovered a number of well-supported clades, including a monophyletic Xanthoidea (BS100/pP100), a broadly defined clade encompassing pseudorhombilids and panopeids (BS93/pP100), and a panopeid clade (BS84/pP100) (Fig. 1).

Within the panopeid clade, there are a number of well- to moderately well-supported subgroups including a clade comprising: (1) the genera *Acantholobulus* Felder & Martin, 2003 and *Metopocarcinus* Stimpson, 1860 (BS93/pP100); (2) *Rhithropanopeus* Rathbun, 1898, *Neopanope* A. Milne-Edwards, 1880
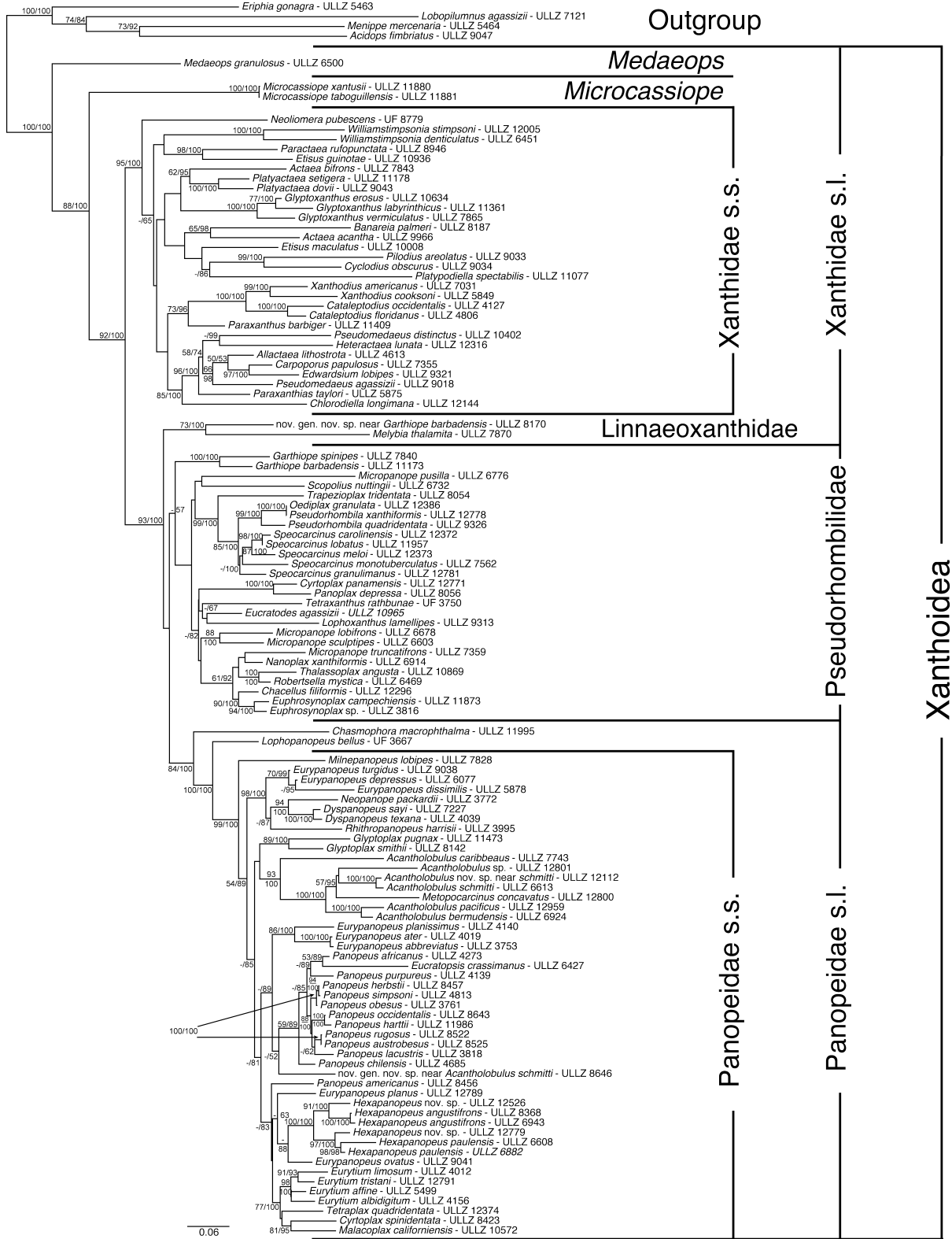
Figure 1. Phylogenetic relationships among selected representatives of Xanthoidea *sensu* Ng *et al.*, 2008 inferred by ML analysis of 2788 bp of a concatenated 12S, 16S, COI, 18S, ENO and H3 dataset. Confidence values are 1000 bootstrap ML values followed by Bayesian posterior probabilities. Values below 50 are indicated by '–'. Brackets and associated names represent the primary clades discussed.

(see Milne-Edwards, 1873–1880), *Dyspanopeus* Martin & Abele, 1986, and several representatives of the genus *Eurypanopeus* A. Milne-Edwards, 1878 (BS98/pP100); (3) *Hexapanopeus angustifrons* (Benedict & Rathbun, 1891), *Hexapanopeus paulensis* Rathbun, 1930, and two previously undescribed species (BS100/pP100); (4) *Eurytium* Stimpson, 1859, *Tetraplax quadridentata* (Rathbun, 1898), *Cyrtoplax spinidentata* (Benedict, 1892), and *Malacoplax californensis* (Lockington, 1877) (Lockington, 1877a) (BS77/pP100); (5) the genus *Eurytium* (BS98/pP100); (6) several Pacific representatives of the genus *Eurypanopeus* [i.e. *Eurypanopeus planissimus* (Stimpson, 1860), *Eurypanopeus abbreviatus* (Stimpson, 1860), and *Eurypanopeus ater* Rathbun, 1930; BS86/pP100]; and (7) a moderately well-supported clade containing *Eucratopsis crassimanus* (Dana, 1851) and 11 representatives of the genus *Panopeus* H. Milne Edwards, 1834 (BS59/pP89).

While overall support for the pseudorhombilid clade is low (BS < 50/pP57), several well-supported clades are recovered within it, including: (1) species of *Garthiope* Guinot, 1990 (BS100/pP100); (2) species of *Speocarcinus* Stimpson, 1859, *Oediplax granulata* Rathbun, 1893, *Pseudorhombila quadridentata* (Latreille, 1828) (see Latreille, 1825–1828), *Pseudorhombila xanthiformis* Garth, 1940, and *Trapezioplax tridentata* (A. Milne-Edwards, 1880) (BS99/pP100); (3) *Micropanope* Stimpson, 1871 (Stimpson, 1871b) (*sensu* Guinot, 1967) (BS88/pP100); (4) *Thalassoplax angusta* Guinot, 1969 and *Robertsella mystica* Guinot, 1969 (BS100/pP100); (5) *Euphrosynoplax campechiensis* Vázquez-Bader & Gracia, 1991, *Euphrosynoplax* sp. and *Chacellus filiformis* Guinot, 1969 (BS90/pP100); and (5) *Cyrtoplax panamensis* Ziesenhenne, in Garth, 1940, and *Panoplax depressa* Stimpson, 1871 (Stimpson, 1871b) (BS100/pP100). Sister to the pseudorhombilid clade is a well-supported clade containing *Melybia thalamita* Stimpson, 1871 (Stimpson, 1871b) and an undescribed genus and species that is morphologically convergent with *Garthiope barbadensis* (Rathbun, 1921) (BS73/pP100).

The family Xanthidae, excluding those taxa shown here to be more closely related to Pseudorhombilidae, is represented by three clades with the bulk of the included xanthid taxa in a single well-supported clade (BS95/pP100) that is sister to the panopeid/pseudorhombilid clade. Sister to this group are two lineages represented in each case by a single genus. One is represented by *Microcassiope xantusii* (Stimpson, 1871) (Stimpson, 1871a) and *Microcassiope taboguillensis* (Rathbun, 1907), which is recovered as the well-supported sister to the larger clade comprising the xanthids, pseudorhombilids, and panopeids (BS88/pP100). The other is sister to all other xanthoids in the analysis and represented by a

single species, *Medaeops granulosus* (Haswell, 1882) (BS100/pP100).

DISCUSSION OF PHYLOGENETIC RELATIONSHIPS

To clarify the phylogenetic relationships among xanthoids from American waters, we collected data from a more diverse set of taxa and applied more genetic markers than used in previous studies (Schubart *et al.*, 2000; Thoma *et al.*, 2009; Felder & Thoma, 2010).

Our molecular phylogenetic analysis, based on partial sequence data from both nuclear (18S, H3, ENO) and mitochondrial (12S, 16S, COI) genes, indicates that the superfamily Xanthoidea *sensu* Ng *et al*. 2008, is monophyletic. All 113 xanthoid taxa were recovered in a single well-supported clade (BS100/pP100), which supports the findings of Lai *et al*. (2011). Xanthoid representatives were distributed among six clades: three large clades, which on morphological bases appear to represent restricted memberships of the xanthoid families Xanthidae, Panopeidae, and Pseudorhombilidae; a clade we postulate to represent the subfamily Linnaeoxanthinae Števčić, 2005; and two smaller clades that we propose to represent previously unrecognized lineages within Xanthoidea.

The outgroup taxa represented here include the families Acidopsidae Števčić, 2005 (Goneplacoidea MacLeay, 1838, see Castro, Guinot & Ng, 2010), Menippidae Ortmann, 1893, Eriphiidae MacLeay, 1838, and Pilumnidae Samouelle, 1819 (Pilumnoidea Samouelle, 1819) (i.e. *Acidops fimbriatus*, *Menippe mercenaria*, *Eriphia gonagra*, and *Lobopilumnus agassizii*, respectively). These taxa were recovered as sister to representatives of the superfamily Xanthoidea in previous analyses (Thoma *et al.*, 2009; Lai *et al.*, 2011; our unpubl. data) and are recovered outside of Xanthoidea in these analyses as well.

Xanthidae *s.l.*

The present analysis includes 47 species representing the family Xanthidae (*sensu* Ng *et al.*, 2008), encompassing representatives for nine of the 13 subfamilies presently thought to comprise the family. Of these nine subfamilies, Liomerinae Sakai, 1976, Zalasiinae Serène, 1968, and Zosiminae Alcock, 1898 are each represented by a single taxon [i.e. *Neoliomera pubescens* (H. Milne Edwards, 1834), *Banareia palmeri* (Rathbun, 1894), and *Platypodiella spectabilis* (Herbst, 1794) (see Herbst, 1782–1804), respectively) making any comment on monophyly of these subfamilies impossible. Of the six xanthid subfamilies represented by two or more taxa in the present analyses, only Speocarcininae Števčić, 2005 is recovered as monophyletic, albeit as part of a clade

unrelated to the bulk of the xanthid taxa (see Pseudorhombilidae *s.l.* below). Although it appears that nearly all of the currently recognized subfamilies are in need of revision, perhaps most problematic is Xanthinae MacLeay, 1838, the subfamily best represented in the present analysis. The 15 taxa representing Xanthinae are recovered in 10 clades, including five small clades within a larger grouping comprised of representatives from all three xanthoid families (see Pseudorhombilidae *s.l.* below). These results are similar to those presented by Lai *et al.* (2011) where 34 species of Xanthinae were recovered in ten clades, including two found within a group similar in composition to the pseudorhombilid clade recovered in the present work.

Medaeops granulosus

Among the five xanthid clades, two groups appear to represent early-branching lineages within the superfamily, distinct from any of the four clades that represent existing xanthoid families. One of these early-branching lineages is represented by *Medaeops granulosus* (see Mendoza, Chong & Ng, 2009). We propose that this lineage probably includes 24 West Pacific and Indo-West Pacific species of the subfamily Euxanthinae Alcock, 1898, recovered as an early-branching lineage in the study by Lai *et al.* (2011; see Clade Eux 3 in their fig. 1). It is unclear how the composition of this clade might change were additional taxa added to the analysis, but it is clear that it represents a lineage distinct from Xanthidae *s.s.* (see below).

Microcassiope

The second of two early-branching xanthid lineages is represented by two species of *Microcassiope* Guinot, 1967 (*M. xantusii* and *M. taboguillensis*). This well-supported lineage (BS88/pP100) is sister to the remaining xanthoids.

The presence of the early-branching lineages of *Microcassiope* and *Medaeops granulosus* suggests that the present classification of the superfamily Xanthoidea is not natural and that the family Xanthidae is in need of further subdivision (Lai *et al.*, 2011). In particular, either the families Panopeidae and Pseudorhombilidae should be considered subfamilies of Xanthidae or many of the xanthid subfamilies should be elevated to familial status within the superfamily Xanthoidea. The recovery of *Microcassiope* as a distinct lineage outside of the family Xanthidae suggests it perhaps represents a separate family; more robust analyses are under way.

Xanthidae s.s.

The bulk of the xanthid species included in the analyses (i.e. 64%) are recovered in a single, large, well-supported clade (BS95/pP100) comprised exclusively of taxa commonly treated as xanthid species. Previous analyses have shown affinities between *Xantho* Leach, 1814, the type genus, and representatives of this larger xanthid clade (Lai *et al.*, 2011). Although *Xantho* is not included in the present analysis, we conclude that this clade represents Xanthidae *s.s.* and consists of several subfamilies (e.g. Xanthinae MacLeay, 1838 emend., Actaeinae Alcock, 1898 emend., Glyptoxanthinae Mendoza & Guinot, 2011, Chlorodiellinae Ng & Holthuis, 2007, Euxanthinae Alcock, 1898); however, most of these subfamilies do not appear to be monophyletic as presently defined.

Despite being a common component of assemblages in tropical and subtropical waters of the Americas, the family Xanthidae is most diverse in tropical West and Indo-west Pacific waters (Forest & Guinot, 1961; Serène, 1984). As we chose to include only American representatives of the family, we do not here comment further on subfamilies within Xanthidae but instead focus on some of the xanthid taxa with putative affinities to Panopeidae and Pseudorhombilidae.

Linnaeoxanthidae

Števčić (2005) described the family Melybiidae Števčić, 2005 to accommodate the monotypic genus *Melybia* Stimpson, 1871b and placed the family within the Portunoidea Rafinesque, 1815 without explanation or justification. Although his brief diagnosis suggests the presence of a 'portunid lobe', our examinations have revealed no evidence of a portunid lobe and support the findings of Ng *et al.* (2008) who recognized *Melybia* as part of Xanthoidea rather than Portunoidea. Števčić (2005) also described the genus *Linnaeoxantho* Števčić, 2005 and erected the subfamily Linnaeoxanthinae within Xanthidae to accommodate *Pilumnoplax acanthomerus* Rathbun, 1911. While Ng *et al.* (2008) recognized the genus *Linnaeoxantho*, they considered it to be part of Xanthinae along with *Melybia*. More recently, Mendoza, Clark & Ng (2012) reviewed the identity of *P. acanthomerus* and agreed with Števčić in recognizing both *Linnaeoxantho* and the subfamily Linnaeoxanthinae, while considering Linnaeoxanthinae and Melybiidae synonyms, and noting the priority of Linnaeoxanthinae.

Lacking *Linnaeoxantho* in the present analyses, our findings cannot address affiliation between *Linnaeoxantho* and *Melybia* as proposed by Mendoza *et al.* (2012). However, if we assume that morphological similarities seen in these two genera reflect shared ancestry and not convergence, then the present analyses indicate a clear relationship between Linnaeoxanthinae and other xanthoid taxa but it does not appear to be part of the family Xanthidae as proposed by Ng *et al.* (2008) or Mendoza

et al. (2012). In the present analysis, *Melybia* is recovered as sister to Pseudorhombilidae in a moderately well-supported clade (BS73/pP100) with an undescribed genus and species that is morphologically similar to *Garthiope barbadensis*. Given the topology presented here and the detailed morphological comparisons presented by Mendoza *et al*. (2012), we conclude that Linnaeoxanthinae (*sensu* Mendoza *et al*., 2012) should be elevated to full family status as a lineage within the Xanthoidea.

Micropanope s.l.

As early as 1880 *Micropanope* was recognized to represent more than a single lineage (A. Milne-Edwards, 1873–1880). Although Guinot (1967) revised the genus, describing five previously unrecognized genera, she suggested that species attributed to *Micropanope* were still representative of multiple distinct lineages. At that time, Guinot suggested that *Micropanope s.s.* should be restricted to *Micropanope sculptipes* Stimpson, 1871b (the type species) and *Micropanope lobifrons* A. Milne-Edwards, 1880 (see Milne-Edwards, 1873–1880), but retained several species within the genus until such time as they could be examined more thoroughly (Guinot, 1967, 1971).

Our analyses, which are largely congruent with previous observations (Guinot, 1967, 1971), indicate that *Micropanope*, as currently defined, represents multiple distinct lineages. *Micropanope sculptipes* and *M. lobifrons* are recovered in a single well-supported clade (BS88/pP100), while *Micropanope pusilla* A. Milne-Edwards, 1880 (see Milne-Edwards, 1873–1880) and *Micropanope truncatifrons* Rathbun, 1898, the other two representatives of the genus included in the analysis, are found in two highly divergent clades. As *M. sculptipes* is the type species of the genus, our findings support restriction of *Micropanope s.s.* to only *M. sculptipes* and *M. lobifrons*, as proposed by Guinot (1967). Although the present analysis suggests that *Micropanope* is not monophyletic and in need of further revision, we await molecular data for remaining species of the genus before a thorough analysis is undertaken. Thus, the status of the tribe Micropanopeini established by Števčić (2005) for the whole genus *Micropanope* (with *M. sculptipes* as type species) and diagnosed by a G1 'straight, tip blunt, stout, distally strongly recurved' remains uncertain. The present analyses support recognition of *Scopolius* Števčić, 2011 for *Micropanope nuttingi* (Rathbun, 1898), with *Scolopius nuttingi* being recovered in a linage distinct from *Micropanope s.s.* as an unsupported sister to *Micropanope pusilla*. While these two taxa are vaguely similar in general habitus, the morphology of G1 clearly separates them, though the topology presented here provides no evidence that the genus *Scolopius* warrants treatment as a the separate tribe, Scopoliini Števčić, 2011.

Although *Micropanope* has more recently been recognized as a part of Xanthidae (Ng *et al*., 2008), historically it has been considered to be a part of the family Panopeidae, and Guinot (1967: 349) has shown that its affinities must be researched among Panopeinae ('ses affinités seraient donc à rechercher parmi les Panopeinae'). In the present analysis all included species of *Micropanope* are recovered within a large clade comprising mostly of pseudorhombilids along with representatives of the other two xanthoid families, which suggests that the genus is more closely allied to pseudorhombilids than to either xanthids or panopeids.

Panopeidae *s.l.*

In the present analysis the family Panopeidae as defined by Ng *et al*. (2008) is not recovered as monophyletic. Several taxa attributed to both subfamilies [i.e. Panopeinae Ortmann, 1893: *Tetraxanthus rathbunae* Chace, 1939, *Lophoxanthus lamellipes* (Stimpson, 1860); Eucratopsinae Stimpson, 1871 (Stimpson, 1871b): *Panoplax depressa*, *Cyrtoplax panamensis*, *Thalassoplax angusta*, and *Robertsella mystica*] are recovered as part of the pseudorhombilid clade (comprising pseudorhombilids and a few representatives of the other two families; see Pseudorhombilidae *s.l.* below). Despite being recovered among the pseudorhombilids, they do not appear to have strong affinities for one another; for instance, *T. angusta* and *R. mystica* form a well-supported clade (BS100/pP100) while *L. lamellipes*, *P. depressa*, *C. panamanensis*, and *Tetraxanthus rathbunae* are all part of an unsupported clade that contains the xanthid *Eucratodes agassizii* A. Milne-Edwards, 1880 (see Milne-Edwards, 1873–1880). As the remaining panopeid taxa included in this study are recovered in a single well-supported clade (BS84/pP100) comprising exclusively panopeid taxa, we suggest that these six taxa are not part of Panopeidae *s.s.* and should be transferred to Pseudorhombilidae as redefined here.

Chasmophora

The panopeid clade appears to comprise several distinct lineages that originate deep within the clade. One is represented by the monospecific genus *Chasmophora* Rathbun, 1914, known from the tropical Eastern Pacific, which has a peculiar set of characters of the G1 and a penis that is completely protected (Guinot, 1969c: 714). Although *Chasmophora* is recovered as the sister to Panopeidae in the phylogenetic analysis, representatives of the genus share several morphological characters with representatives of Pseudorhombilidae. It is unclear if these similarities, which include a G1 (see Guinot,

1969c: figs 1, 3, 4a–e) with a convoluted, vaguely foliform apex (not resembling the typical trifid arrangement typically found in Panopeidae) and a male thoracic sternum that is much broader than long in the anterior portions, are the result of convergence or indicate the shared ancestry of the pseudorhombilids and *Chasmophora*.

When discussing *Chasmophora* as part of his morphologically based reclassification of Brachyura, Števčić (2005) recognized Chasmophorinae Števčić, 2005, as a distinct lineage within Pseudorhombilidae. While the present analysis supports recognizing *Chasmophora* as a distinct lineage, it appears to be more closely related to panopeids than to the pseudorhombilids, a hypothesis suggested with reservation by Guinot (1969c). Based upon the phylogenetic relationships depicted here and the contradictory interpretations of morphology, we defer judgment on the affinities of *Chasmophora* until morphological evidence can be thoroughly reevaluated.

Lophopanopeus

Lophopanopeus bellus (Stimpson, 1860), the type species of the genus, is recovered as another early-branching sister to the remaining panopeids. This eastern Pacific group currently comprises eight species. Although only a single species was included in the present analysis, *Lophopanopeus* Rathbun, 1898 appears to represent a distinct lineage outside Panopeinae. In addition to sampling additional representatives of the group in molecular analyses, morphology of this genus must be further examined for evidence that may distinguish it from other Panopeinae.

Panopeidae *s.s.*

A well-supported clade (BS99/pP100), which we regard to represent Panopeidae *s.s.*, is recovered in this analysis and is similar in composition to those in previous analyses (Thoma *et al.*, 2009; Felder & Thoma, 2010). Within Panopeidae *s.s.*, several generic-level clades [i.e. *Hexapanopeus* Rathbun, 1898 *s.s.* (BS100/pP100), *Eurytium* (BS98/pP100), *Glyptoplax* Smith, 1870 (BS89/pP100), and *Dyspanopeus* (BS100/pP100)], are recovered as monophyletic groups, much as in previous analyses (see Thoma *et al.*, 2009). However, we did not expect to find *Eucratopsis* Smith, 1869 within a larger clade comprising species of *Panopeus* (see *Panopeus* below). The genus *Eurypanopeus* also continues to prove problematic (Schubart *et al.*, 2000; Thoma *et al.*, 2009), as representatives of the genus are recovered in five different clades within Panopeidae. In addition, the panopeid subfamilies, Eucratopsinae and Panopeinae, are not recovered as monophyletic in the present analysis. However, several genera attributed

to Eucratopsinae are recovered in a monophyletic clade and appear to be united by unique characters of the male thoracic sternum (see *Tetraplax* Rathbun, 1901, *Cyrtoplax* Rathbun, 1914 and *Malacoplax* Guinot, 1969 below).

Panopeus

Several studies have indicated that *Panopeus americanus* Saussure, 1857 represents a lineage distinct from that of *Panopeus s.s.* (Schubart *et al.*, 2000; Thoma *et al.*, 2009). Therefore, it is not surprising to find *P. americanus* well separated from its congeners included in the present analysis. Here it is recovered as sister to a clade comprising several species of *Eurypanopeus* [*Eurypanopeus planus* (Smith, 1869) and *Eurypanopeus ovatus* (Benedict & Rathbun, 1891)], *Hexapanopeus*, *Eurytium*, *Tetraplax*, *Malacoplax*, and *Cyrtoplax spinidentata*, although this topology is not well supported (BS < 50/pP83). In addition to the genetic differences, morphology of the G1 of *P. americanus* is quite different from that in typical species of *Panopeus* (type species: *Panopeus herbstii* H. Milne Edwards, 1834). While its affinities within the family remain unclear, *P. americanus* is clearly not representative of *Panopeus s.s.*

Whereas the remaining representatives of *Panopeus* (i.e. excluding *P. americanus*) are recovered in a single clade, overall support for the arrangement is low (BS59/pP89) and a single representative of *Eucratopsis crassimanus* is recovered nested deep within this clade as the sister-taxon of *Panopeus africanus*. *Eucratopsis* was long considered representative of Goneplacoidea MacLeay, 1838 and is readily separated from *Panopeus* based on the morphology of the carapace and chelipeds (e.g. Smith, 1869; Rathbun, 1918; Guinot, 1969a; Williams, 1984). However, Martin & Abele (1986: 191) pointed out that the G1s of *E. crassimanus* 'are of the *Panopeus* form', but did not elaborate. As our analyses is the first to include genetic data from representatives of *E. crassimanus* it is unclear if the present arrangement is an artefact of the analyses or reflective of the shared ancestry. To ensure that the present arrangement of *E. crassimanus* did not result from contamination or other error, multiple specimens of *E. crassimanus* were included in preliminary analyses of individual genes and combined datasets, all of which revealed similar topologies. In addition, sequences were examined for differences in GC ratios to ensure that this relationship did not reflect convergence as a result of GC bias in the mitochondrial data (12S, 16S, and COI).

Present analyses suggest that *Panopeus*, exclusive of *P. americanus*, represents four distinct lineages including: (1) *Panopeus chilensis* H. Milne Edwards & Lucas, 1843 (see Milne Edwards & Lucas, 1842–1844);

(2) *Panopeus purpureus* Lockington, 1877 (Lockington, 1877b); (3) *P. africanus*; and (4) *Panopeus lacustris* Desbonne, in Desbonne & Schramm, 1867, *Panopeus austrobesus* Williams, 1983, *Panopeus rugosus* A. Milne-Edwards, 1880 (see Milne-Edwards, 1873–1880), *Panopeus harttii* Smith, 1869, *Panopeus occidentalis* Saussure, 1857, *Panopeus obesus* Smith, 1869, *Panopeus simpsoni* Rathbun, 1930, and *P. herbstii* H. Milne Edwards, 1834 (type species). As morphological characters traditionally used in delineating species of *Panopeus* have not proven useful, additional studies, both genetic and morphological, are needed to further clarify evolutionary relationships of the species attributed to the genus.

The specific status of *Panopeus simpsoni*, *P. obesus*, and, to a lesser extent, *P. lacustris*, has long been debated (Rathbun, 1930; Turner & Lyerla, 1980; Reames & Williams, 1983; Sullivan *et al.*, 1983; Williams, 1983, 1984; Schubart *et al.*, 2000). Initially described as forms of *Panopeus herbstii*, these taxa were elevated to full species status by Williams (1983) based upon allozyme, haemocyanin, ecological, and morphological differences. However, Schubart *et al.* (2000) pointed out that 16s rRNA does not distinguish between *P. herbstii* and *P. simpsoni* and furthermore provided only a single nucleotide position to distinguish *P. obesus* from these two taxa. Despite these similarities, the authors chose not to synonymize *P. simpsoni* with *P. herbstii*. While the present phylogenetic analysis provides little additional support for maintaining species status for *P. simpsoni*, examination of COI alignments provides some support for the conservative approach taken by Schubart *et al.* (2000), with five nucleotide differences between *P. herbstii* and *P. simpsoni*. Regardless, it appears that these three taxa have only recently diverged as few mutations have accumulated in the examined sequences.

Eurypanopeus s.l.
Previous analyses of *Eurypanopeus* have concluded the genus was not monophyletic (Schubart *et al.*, 2000; Thoma *et al.*, 2009); therefore, it is not surprising to find that the eight representatives of the genus included in this study are recovered in four widely separated clades. Six of these eight taxa are recovered in two clades comprising: (1) *Eurypanopeus turgidus* (Rathbun, 1930), *Eurypanopeus depressus* (Smith, 1869), and *Eurypanopeus dissimilis* (Benedict & Rathbun, 1891) (BS70/pP99) and (2) *Eurypanopeus ater*, *Eurypanopeus abbreviatus*, and *Eurypanopeus planissimus* (BS86/pP100). Two additional lineages, each represented by a single taxon (i.e. *Eurypanopeus ovatus* and *Eurypanopeus planus*, respectively), are recovered as early branching lineages near the base of the *Hexapanopeus s.s.* clade.

Eurypanopeus ovatus is recovered as the sister-taxon to *Hexapanopeus s.s.* Despite the lack of support for this relationship (BS < 50/pP88), it is worth noting that in their analysis, Schubart *et al.* (2000) recovered a similar relationship between *Eurypanopeus crenatus* (H. Milne Edwards, 1834), the type species of the genus, and *Hexapanopeus s.s.* This suggests that *E. ovatus* and *E. crenatus*, both eastern Pacific species, may represent *Eurypanopeus s.s.* and that both *E. abbreviatus* and *E. depressus* may represent yet undefined genera. However, until thorough genetic and morphological analyses of all 14 species of the genus can be undertaken, we conclude only that *Eurypanopeus* is not monophyletic.

Although *Eurypanopeus turgidus* was long recognized as a member of the genus *Panopeus*, the analysis of Schubart *et al.* (2000) recovered it as a close relative of *E. depressus*, well separated from representatives of *Panopeus*. In the present analysis, *E. turgidus* is recovered as the sister to a clade comprising *E. depressus* and *E. dissimilis*. While support for this clade is fairly strong (BS70/pP99), the support for the sister-taxa relationship between *E. depressus* and *E. dissimilis* is less clear despite similarities in morphology long thought to reflect their proximity (Rathbun, 1930). As *Eurypanopeus turgidus* is clearly not related to *Panopeus*, we consider it part of *Eurypanopeus* until a thorough review of the group can be undertaken.

The clade composed of *Eurypanopeus ater*, *E. abbreviatus*, and *E. planissimus* is recovered as sister to a clade comprising *Panopeus* and *Eucratopsis* (see '*Panopeus*' above). Although this arrangement is not well supported (BS < 50/pP89), there is little doubt that the '*Eurypanopeus abbreviatus*' clade is only distantly related to the other members of *Eurypanopeus* in the present analysis (see also Schubart *et al.*, 2000; Thoma *et al.*, 2009).

Hexapanopeus s.l.
The genus *Hexapanopeus* has been shown in previous analyses (Thoma *et al.*, 2009) to be not monophyletic. However, recent revisions of the group, including the transfer of *Hexapanopeus caribbaeus* Stimpson, 1871 (Stimpson, 1871a) to *Acantholobulus* (see Thoma *et al.*, 2009) and the description of *Milnepanopeus* Thoma & Felder, 2012 to accept *Hexapanopeus lobipes* (A. Milne-Edwards, 1880) (see Milne-Edwards, 1873–1880), have helped to further refine and clarify the species composition of the genus. Pending genetic and morphological analysis, seven eastern Pacific species have been tentatively retained in *Hexapanopeus*. Preliminary morphological analyses of these eastern Pacific taxa suggest that *Hexapanopeus costaricensis* Garth, 1940, *Hexapanopeus cartagoensis* Garth, 1939, and *Hexapanopeus sinaloensis* Rathbun, 1930 have a

G1 that is morphologically similar to that of *Glyptoplax pugnax* Smith, 1870, the type species of *Glyptoplax*, and that these species may be more representative of *Glyptoplax* than they are of *Hexapanopeus*. In addition, examination of G1 morphology suggests that *Hexapanopeus orcutti* Rathbun, 1930 and *Hexapanopeus rubicundus* Rathbun, 1933 may better fit *Acantholobulus* than *Hexapanopeus*. As specimens suitable for genetic analysis have yet to become available for these seven Pacific species, we must defer judgment.

Another potentially problematic taxon is an undescribed species with morphological similarities to *Acantholobulus schmitti* (Rathbun, 1930) (formerly *Hexapanopeus schmitti*). In previous analyses, specimens attributed to this species (as gen. nov., sp. nov. near *Acantholobulus schmitti* – ULLZ 8646) have shown affinities to both *Glyptoplax smithii* A. Milne-Edwards, 1880 (see Milne-Edwards, 1873–1880) (based on 12S rRNA; fig. 2 in Thoma *et al*., 2009) and *Hexapanopeus s.s.* (16S rRNA; fig. 1 in Thoma *et al*., 2009); however, neither of these arrangements was well supported. In the present analyses, 'gen. nov., sp. nov. near *Acantholobulus schmitti* – ULLZ 8646' is recovered as the sister-taxon to a clade comprising *Panopeus* and *Eucratopsis* (see *Panopeus* above), although this topology has no support from either ML or Bayesian analyses. The phylogenetic affinities of this taxon remain uncertain as it appears to lack strong genetic ties to any known panopeid genus and, despite its morphological similarities to *A. schmitti*, there is no evidence from genetic analyses to support this relationship. Until detailed morphological examinations can be completed it is unclear if this undescribed taxon is a representative of a known genus or is better accommodated by the establishment of a new genus.

Hexapanopeus s.s.

The present analysis and previous analyses of the group (Thoma *et al*., 2009) suggest that *Hexapanopeus s.s.* consists of only two nominal species, *Hexapanopeus angustifrons* and *Hexapanopeus paulensis*, as well as several undescribed lineages. Both *H. angustifrons* and *H. paulensis*, as currently defined, appear to comprise two or more cryptic species (Thoma *et al*., 2009), a finding that is supported here as well. In addition, two undescribed species can be attributed to *Hexapanopeus*, including one from the tropical western Atlantic and another from the tropical eastern Pacific. Interestingly, the morphology of the G1 of the specimen from the eastern Pacific is intermediate between that of *H. orcutti* and the G1 figured from a specimen referred to as *Panopeus* sp. by Martin & Abele (1986, see their fig. 2B). It remains to be seen whether this similarity in morphology is indicative of convergence or shared ancestry between *H. orcutti* and the undescribed lineage of *Hexapanopeus* from the eastern Pacific.

Acantholobulus s.l.

Although previous analyses of *Acantholobulus* have indicated the genus is monophyletic (Thoma *et al*., 2009), the inclusion of *Metopocarcinus concavatus* Crane, 1947 in the present analysis suggests that it may comprise three or more lineages. Originally erected to accommodate four representatives of *Panopeus* and *Hexapanopeus* due to similarities in carapace and G1 morphology as well as general habitus (Felder & Martin, 2003), *Acantholobulus* now includes five species: *Acantholobulus bermudensis* (Benedict & Rathbun, 1891) (type species), *Acantholobulus pacificus*, *Acantholobulus miraflorensis* (Abele & Kim, 1989), *Acantholobulus schmitti*, and *Acantholobulus caribbaeus* (see Felder & Martin, 2003; Thoma *et al*., 2009 for summaries). All representatives of *Acantholobulus*, omitting *A. miraflorensis* (not included in the present analysis), are found in a well-supported clade (BS93/pP100) with *M. concavatus* and an undescribed species from the Eastern Pacific (i.e. *Acantholobulus* sp. – ULLZ 12801).

The representatives of *Acantholobulus* and *M. concavatus* differ in carapace morphology but have similar morphology of the G1. In addition, both taxa can be found readily in similar habitats (i.e. subtropical to tropical, intertidal to shallow subtidal, fouled/rubble habitats) but have no apparent overlap in distribution. Whether these similarities to any extent justify synonymizing *Acantholobulus* with *Metopocarcinus* must await more detailed morphological analyses.

Eucratopsinae

Guinot (1978) separated Panopeidae into two groups: (1) panopeids with 'xanthian facies' (faciès 'xanthien') (taxa formerly in Xanthinae or Pilumninae) and male genital openings that are coxal (i.e. not passing through an elongate groove between sternites 7 and 8) and (2) panopeids with 'goneplacid facies' (faciès 'gonéplacien') (taxa formerly in Goneplacidae: Prionoplacinae Alcock, 1900 by Balss, 1957) and male genital openings that range from coxal (as in Panopeinae) to coxo-sternal (i.e. passing through an elongate groove between sternites 7 and 8 and often covered ventrally by a portion of the sternites 7 and/or 8). Guinot (1978) conditionally recognized the names Panopeinae Ortmann, 1893 and Eucratopsinae Stimpson, 1871 for these two groups, respectively.

These subfamilies must be revised as both the present phylogenetic analyses and previous work by Thoma *et al*. (2009) have shown the subfamilies, as

presently described, are not monophyletic. Of the 13 genera attributed to Eucratopsinae by Guinot (1978) and refined by Ng *et al.* (2008), nine are included in the present analyses: *Cyrtoplax*, *Tetraplax*, *Eucratopsis*, *Glyptoplax*, *Malacoplax*, and *Panoplax* Stimpson, 1871 (Stimpson, 1871b), *Robertsella* Guinot, 1969, *Thalassoplax* Guinot, 1969, and *Chasmophora*. Representatives of these taxa are recovered in six highly divergent clades.

As mentioned above (see *Panopeus*), *Eucratopsis crassimanus*, the type species of the type genus of the subfamily Eucratopsinae, is recovered within a clade comprising species of the type genus of Panopeinae (*Panopeus*). With the type species of the type genera of both subfamilies being recovered in a single clade, our results suggest that the subfamilies of Panopeidae are not monophyletic. Although two other members of the subfamily Eucratopsinae (i.e. *Chasmophora* and *Glyptoplax*) are recovered within Panopeidae *s.l.*, neither appears to be closely related to *Eucratopsis*. Furthermore, several taxa presently attributed to Eucratopsinae (i.e. *Thalassoplax*, *Robertsella*, *Panoplax*, and *Cyrtoplax panamensis*) are recovered in the pseudorhombilid clade (see Pseudorhombilidae *s.l.* below) suggesting that they are more closely related to Pseudorhombilidae than to Panopeidae *s.s.*

As part of his reclassification of Brachyura, Števčić (2005) erected the tribe Malacoplacini Števčić, 2005 and designated *Malacoplax* as the type genus; however, he neither provided insight into other potential members of the group nor commented on its relationship to the remainder of the family. In our analysis, *Malacoplax* is recovered in an unsupported clade with *Cyrtoplax spinidentata* and *Tetraplax quadridentata*. In addition to being similar in general habitus, these three taxa have a portion of the penis visible between sternites 7 and 8. Although this is not unique to these three taxa, the degree to which the penis is exposed appears to be greater in these than in other taxa. While this clade may be seen as support for Malacoplacini, its distance from other eucratopsid taxa in the present analysis further calls into question the validity of the panopeid subfamilies.

Pseudorhombilidae *s.l.*

Pseudorhombilidae has long been a complex and controversial taxon (Alcock, 1900; Guinot, 1969c, 1971; Hendrickx, 1998; Martin & Davis, 2001; Ng *et al.*, 2008; Felder *et al.*, 2009; De Grave *et al.* 2009). Upon its original description, Alcock (1900) placed Pseudorhombilinae Alcock, 1900 within Goneplacidae MacLeay, 1838 and recognized nine genera within the subfamily, many of which are now considered parts of other families or superfamilies [i.e. *Carcinoplax* H. Milne Edwards, 1852 and *Psopheticus* Wood-Mason,

1892, now in Goneplacidae; *Platypilumnus* Alcock, 1894, now in Mathildellidae Karasawa & Kato, 2003; *Eucrate* De Hann, 1835, now in Euryplacidae Stimpson, 1871 (Stimpson, 1871b); *Litocheira* Kinahan, 1856, now in Litocheiridae Kinahan, 1856; *Catoptrus* A. Milne-Edwards, 1870 and *Libystes* A. Milne-Edwards, 1867, now in Portunidae Rafinesque, 1815; see Castro 2007; Castro & Ng 2008, 2010; Castro *et al.*, 2010; Low *et al.*, 2012; Ng & Manuel-Santos, 2007; Ng *et al.*, 2008; Türkay, 1983).

When preliminarily reviewing the Goneplacoidae, Guinot (1969a–c) pointed out that representatives of Pseudorhombilinae, much like Panopeinae, showed various character states of penis protection. These range from a short penis that is close to the P5 coxal gonopore (as in the cyclometopous disposition) and lies in a shallow depression, to a longer penis that lies in a distinct groove between sternites 7 and 8. In many cases, the penis is protected to some degree by the expansion of sternites 7 and 8 with the most derived coxo-sternal condition typified by the expansion of sternites 7 and 8 until they completely enclose the penis. Although Guinot (1969a–c) pointed out similarities between Pseudorhombilinae and Xanthidae, she tentatively retained the subfamily within the family Goneplacidae.

While describing a new genus and species from the Gulf of California, Hendrickx (1998)) recognized the family Pseudorhombilidae for a group of six genera (*Nanoplax* Guinot, 1967, *Chacellus* Guinot, 1969, *Bathyrhombila* Hendrickx, 1998, *Euphrosynoplax* Guinot, 1969, *Oediplax* Rathbun, 1894, and *Pseudorhombila* H. Milne Edwards, 1837), but it was not until the revision by Martin & Davis (2001) that both Pseudorhombilidae and Panopeidae were recognized as families within Xanthoidea. Several previous phylogenetic analyses have provided support for this arrangement with representatives of Pseudorhombilidae being recovered within Xanthoidea (i.e. Felder & Thoma, 2010; Lai *et al.*, 2011). In the present study all included representatives of Pseudorhombilidae are recovered within Xanthoidea, further supporting recognition this previously ill-defined group as a family within Xanthoidea.

While the taxonomic composition of Pseudorhombilidae has been debated and revised, no review to date has suggested Pseudorhombilidae to be as taxonomically broad as is indicated in the present phylogenetic analysis. Our study finds all included representatives of Pseudorhombilidae in a single clade along with representatives from both panopeid subfamilies and two subfamilies of Xanthidae. Although it remains unclear what the final composition of Pseudorhombilidae will be as additional taxa are included in analyses, it is here proposed that Pseudorhombilidae is both much larger than previously regarded and that it

appears to be the monophyletic sister taxon to the Panopeidae.

As part of his reclassification of Brachyura, Števčić (2005) recognized four subfamilies in Pseudorhombilidae: Pseudorhombilinae Alcock, 1900, Trapezioplacinae Števčić, 2005 (with *Trapezioplax* Guinot, 1969 as the type genus), Tetraxanthinae Števčić, 2005, and Chasmophorinae Števčić, 2005 (see Panopeidae *s.l.*, above). *Trapezioplax tridentata*, the type species of *Trapezioplax*, is recovered in a well-supported clade (pP100/BS99) with *Pseudorhombila quadridentata*, the type species of Pseudorhombilinae, *Oediplax granulata*, and five species of *Speocarcinus*. The proximity of *Trapezioplax* Guinot, 1969 to the type species of the Pseudorhombilinae calls into questions the subfamilial status of Trapezioplacinae.

Tetraxanthus Rathbun, 1898 is clearly part of Pseudorhombilidae, although its relationship to the remainder of the family remains less clear. Although *Tetraxanthus* is recovered in a clade with *Crytoplax*, *Panoplax*, *Eucratodes* A. Milne-Edwards, 1880 (see Milne-Edwards, 1873–1880), and *Lophoxanthus* A. Milne-Edwards, 1879, (see Milne-Edwards, 1873–1880) the clade has no support (BS < 50/pP < 50). Until additional analyses can include the type species of the group, *Tetraxanthus bidentatus* (A. Milne Edwards, 1880) (see Milne-Edwards, 1873–1880), and relationships of the group can be clarified, we defer judgment on the validity of Tetraxanthinae.

Five of the seven tribes of the subfamily Pseudorhombilinae recognized by Števčić (2005) are represented in this analysis. Representatives of Thalassoplacini Števčić, 2005, Euphrosynoplacini Števčić, 2005, Robertsellini Števčić, 2005, and Chacellini Števčić, 2005 (i.e. four of the five included tribes) are recovered in a single, moderately well-supported clade (pP61/BS92) along with *Nanoplax xanthiformis* (A. Milne-Edwards, 1880) and *Micropanope truncatifrons*. The proximity of these four tribes to one another and the distance from this clade to the representatives of the fifth tribe, Pseudorhombilini Števčić, 2005, suggests that these tribes may be best represented by the rank of genus rather than tribe.

Materials definitively assignable to *Krunorhombila ometlanti* (Vázquez-Bader & Gracia, 1995), the type species of *Krunorhombila* Števčić, 2011, were not available for inclusion in our present phylogenetic analysis. However, comparison of its generic diagnosis to materials of *Pseudorhombila quadridentata*, the type species of *Pseudorhombila*, suggests that *Krunorhombila* is a junior synonym of *Pseudorhombila*. Furthermore, morphological characters used to distinguish between *P. ometlanti* and *P. quadridentata* in the original description of *P. ometlanti* appear to inconsistently exceed grades of intra-specific variation seen in our presently available materials of *P.*

quadridentata, at the very least underlining the proximity of these taxa. Although additional comparisons are needed, including detailed examination of type materials and molecular phylogenetic analyses that represent both of these putatively separate species, present morphological comparisons at minimum do not support recognition of *Krunorhombila* and thus Krunorhombilini is not supported.

DISCUSSION OF ADULT MORPHOLOGY

A number of recent studies have suggested that many of the morphological characters historically used in defining xanthoid taxa (e.g. anterolateral detention of the carapace, modalities of penis protection, chelipeds, and third maxillipeds) appear to be the result of convergence (e.g. Guinot, 1967, 1969a–c, 1978; Schubart *et al.*, 2000; Felder & Martin, 2003; Ng *et al.*, 2008; Thoma *et al.*, 2009; Lai *et al.*, 2011; Thoma & Felder, 2012; Lasley *et al.*, 2013). The present study further confirms the need for a substantial revision of the group, particularly the subfamilies of Xanthidae. Although a complete revision is beyond the focus of this study, there are a number of morphological characters that show promise in defining clades recovered in our preliminary examinations.

Xanthidae *s.l.*

Although the present analysis indicates that the family Xanthidae, as presently defined, is not monophyletic, the topology included several clades comprising taxa presently attributed to the family. Some of these clades (i.e. '*Medaeops granulosus*' clade and '*Microcassiope*' clade) consist of only one or two taxa, making detailed morphological comparisons impractical until analyses of the superfamily combining Old and New World taxa clarify the taxonomic composition of these clades on a global scale.

Xanthidae *s.s.*

Preliminary morphological analyses suggest that American representatives of Xanthidae *s.s.* are united by several characters of the male thoracic sternum and the pereopods of both sexes. In males, no portion of sternite 8 is visible lateral to the abdomen (Fig. 2A, B), while it appears that in males of all other nominal xanthoid families at least some portion of sternite 8 is visible laterally (Fig. 2C–F). Secondly, in at least American representatives of the family, the last walking leg has a dactylus with a distinct subterminal, calcareous tooth on the flexor margin (Fig. 3A), which does not appear to be found in other xanthoids (Fig. 3B, C).

Panopeidae and Pseudorhombilidae

Along with representatives of several lineages previously attributed to the family Xanthidae (see
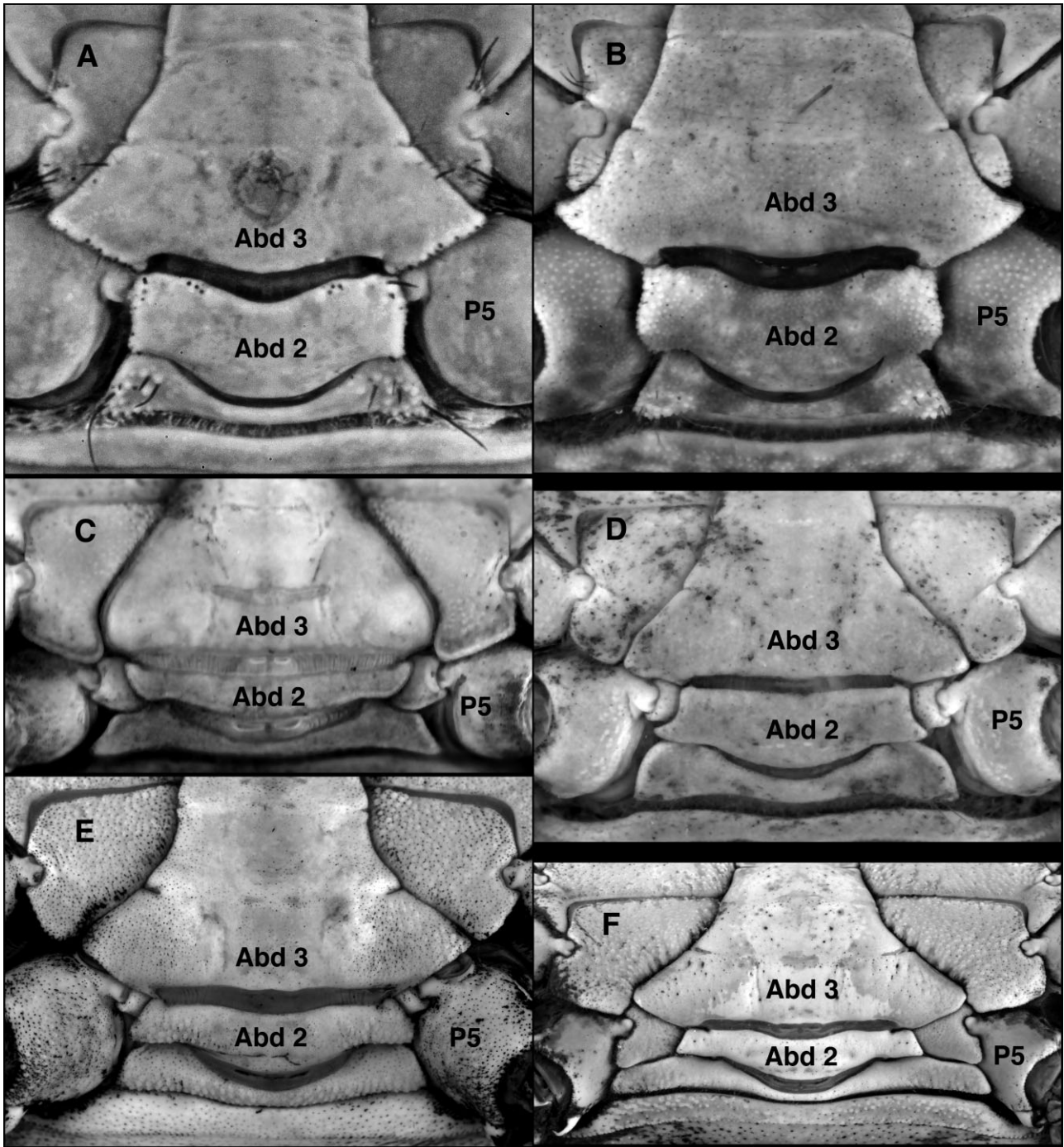
Figure 2. Ventral view of the posterior portion of the thoracic sternum and male abdomen. A, *Etisus maculatus* (ULLZ 10008); B, *Cataleptodius occidentalis* (ULLZ 4127); C, *Rhithropanopeus harrisii* (ULLZ 3995); D, *Panopeus herbstii* (ULLZ 8457); E, *Chacellus filiformis* (ULLZ 12296); F, *Pseudorhombila quadridentata* (ULLZ 9326). Second and 3rd abdominal somites and the coxa of the 5th pereopod are labelled as Abd 2, Abd 3, and P5, respectively.

Linnaeoxanthidae and *Micropanope* above), Panopeidae and Pseudorhombilidae appear to be characterized by males with at least some portion of thoracic sternite 8 visible lateral to the abdomen (Fig. 2C–F).

In addition, representatives of this family lack the distinct subterminal, calcareous tooth found on the dactylus of the last walking leg of American xanthids (Fig. 3B, C).
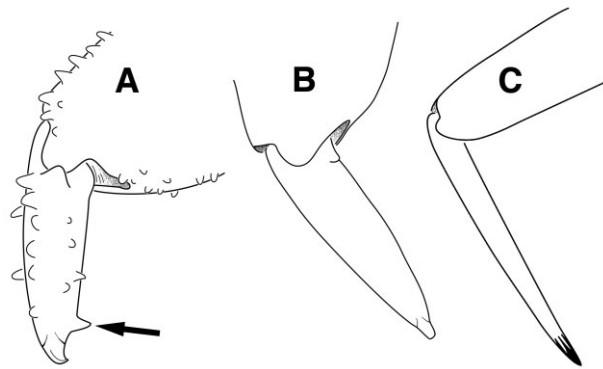
Figure 3. Stylized drawing of the dactylus of the 5th pereopod. A, typical American xanthid; B, typical panopeid; C, typical pseudorhombilid. Arrow indicates distinct, subterminal, calcareous tooth.

Panopeidae

Representatives of Panopeidae *s.s.* are united by having a G1 with a trifid arrangement distally (Fig. 4C, D). In addition it appears that most panopeid lineages have undergone a narrowing of the male thoracic sternum. As a result of this narrowing, anterior portions of the sternum are relatively long and narrow (length/width > 0.60) (Fig. 5A, B). Although there are several exceptions (e.g. *Malacoplax californiensis* and *Cyrtoplax spinidentata*), it appears that a narrowing of the anterior half of the male thoracic sternum serves to quickly separate most representatives of Panopeidae from representatives of Pseudorhombilidae.

Pseudorhombilidae

Male representatives of Pseudorhombilidae appear to share several attributes including a G1 with a convoluted, vaguely folious apex (Fig. 4A, B) and a thoracic sternum that is relatively broad and short in the anterior portions (length/width < 0.60) (Fig. 5C, D). The coxo-sternal condition offers numerous character states in the family Pseudorhombilidae, with transitional patterns and a fully developed penis protection in some taxa (coxo-sternal disposition) (Guinot, Tavares & Castro, 2013). For example, *Bathyrhombila* Hendrickx, 1998 (Hendrickx, 1998: 639, fig. 2B) shows a plesiomorphic condition, whereas the condition varies within the genus *Pseudorhombila* itself, depending on the degree of connection between thoracic sternites 7 and 8, which are not completely joined in *P. xanthiformis* (see Hendrickx 1995: fig. 1C) but completely joined in *P. octodentata* (Rathbun, 1906) (Guinot, 1969c: 113; Hendrickx 1995: fig. 1A), and *P. quadridentata* (Latreille, 1828). Although there appear to be a few taxa that have a thoracic sternum

more typical of panopeids (e.g. *Nanoplax xanthiformis*, *Thalassoplax angusta*, *Micropanope sculptipes*, and *Garthiope spinipes*), the morphology of the first gonopod appears to be a reliable character in distinguishing representatives of the group.

CONCLUSIONS

The present phylogenetic analyses of partial sequences of six genes (i.e. three mitochondrial and three nuclear) indicate that the superfamily Xanthoidea is monophyletic. However, it appears that representatives of the group are in need of detailed systematic revision at all levels (i.e. species to family). In particular, all three families (i.e. Xanthidae, Panopeidae, and Pseudorhombilidae) are recovered as not monophyletic, as are many of the nominal subfamilies and genera.

Morphologically, Xanthoidea remains problematic with the characters useful in delineating the major families remaining elusive. We have here suggested that width of the male abdomen relative to the thoracic sternum, relative proportions of the anterior thoracic sternum, and shape of the first gonopod may prove useful characters for separations; however, there are a number of exceptions to group definitions based upon these characters. In addition, all of the characters that we have thus far uncovered are found only in males of the groups, with the exception of the subterminal, raptorial, calcareous tooth on the dactylus of the last walking leg (P5) found in most American xanthids. As additional taxa are added to this analysis, morphological characters useful in grouping both males and females may be discovered.

While this work provides a foundation for future revision of the group, preliminary morphological analyses have in many cases proven incongruent with our data. Characters traditionally used in the group, such as those of the carapace, modalities of penis protection, chelipeds, and third maxillipeds, have thus far proven to be unreliable in delineating many of the clades inferred from genetic data. Before systematic revision of the group can be undertaken, detailed morphological examinations are necessary to determine which, if any, characters are congruent with the outcomes of molecularly based phylogenetic analyses.
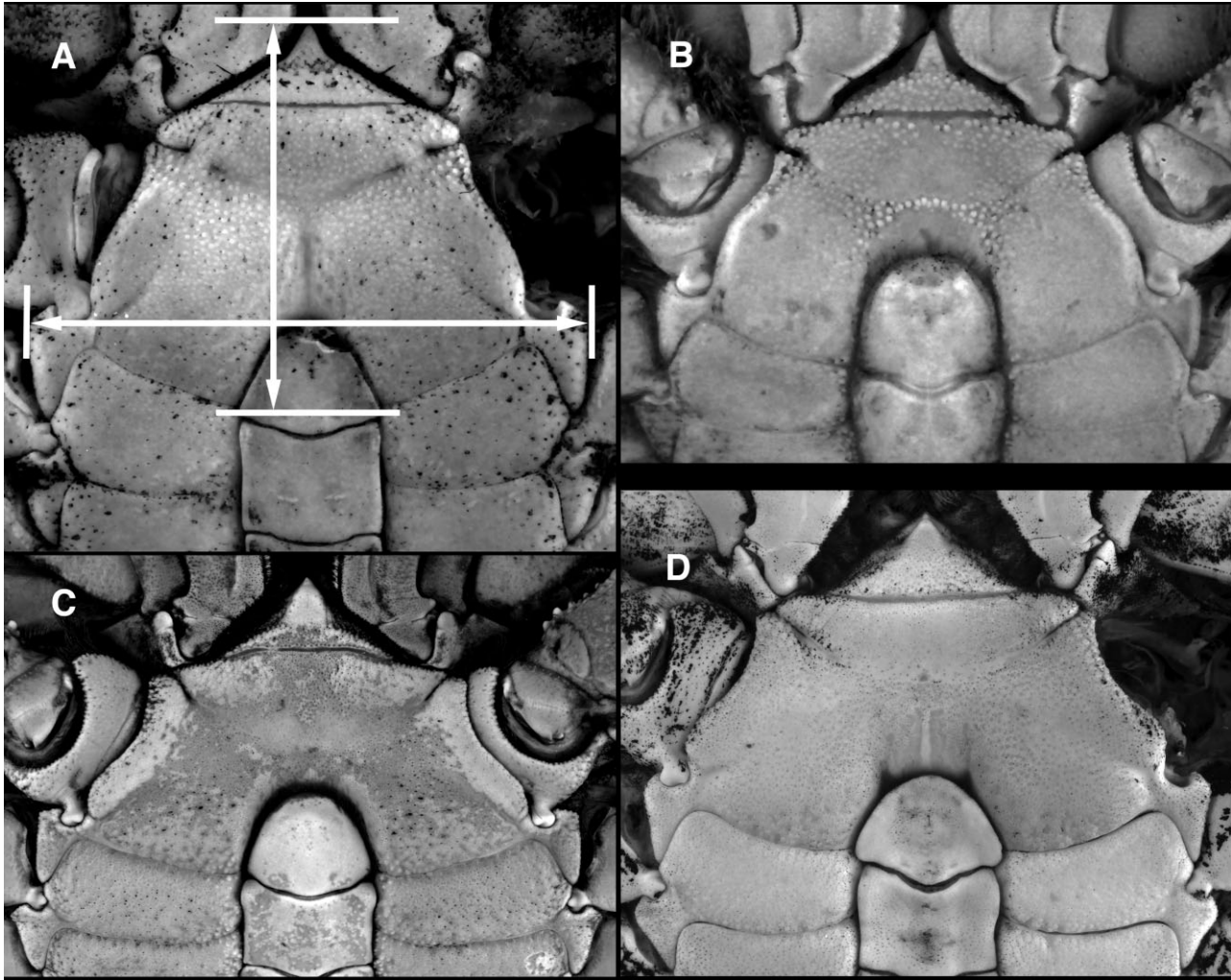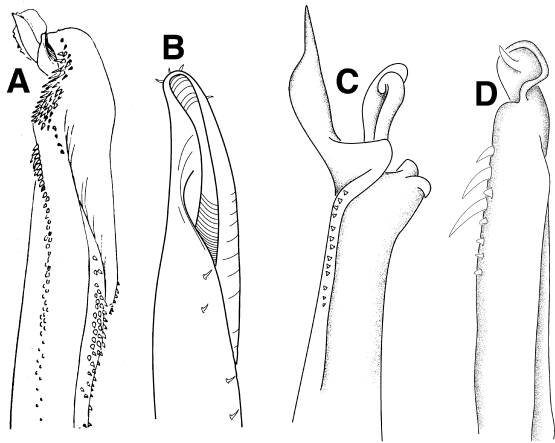
Figure 4. Apex of the first gonopod (first male pleopod). A, *Pseudorhombila quadridentata* (ULLZ 9326); B, *Chacellus filiformis* (ULLZ 12296); C, *Panopeus herbstii* (ULLZ 8457); D, *Rhithropanopeus harrisii* (ULLZ 3995). Arrows and lines indicate measurements taken for preliminary morphometric analyses of sternal proportions.

Figure 5. Ventral view of the anterior portion of the thoracic sternum. A, *Panopeus herbstii* (ULLZ 8457); B, *Rhithropanopeus harrisii* (ULLZ 3995); C, *Pseudorhombila quadridentata* (ULLZ 9326); D, *Chacellus filiformis* (ULLZ 12296). Lines in A indicate the length and width dimensions of the anterior portion of the thoracic sternum.

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