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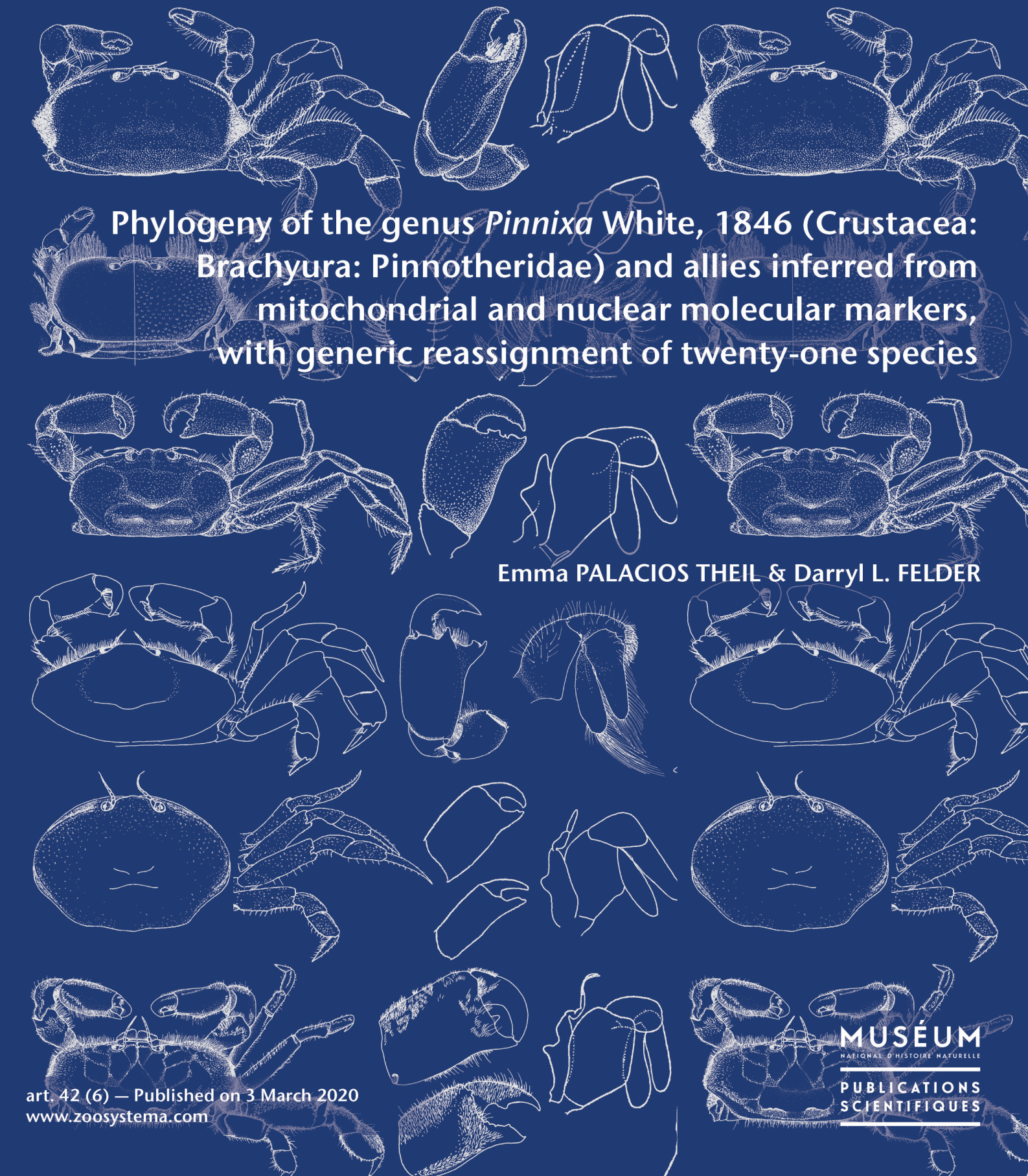

Phylogeny of the genus *Pinnixa* White, 1846 (Crustacea: Brachyura: Pinnotheridae) and allies inferred from mitochondrial and nuclear molecular markers, with generic reassignment of twenty-one species

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Phylogeny of the genus *Pinnixa* White, 1846 (Crustacea, Brachyura, Pinnotheridae) and allies inferred from mitochondrial and nuclear molecular markers, with generic reassignment of twenty-one species

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ABSTRACT
We used mitochondrial 16S-NADH1 complex, mitochondrial 12S, and nuclear histone 3 genes to infer a molecular-based phylogeny, which allowed us to study phylogenetic relationships between species of *Pinnixa* White, 1846 *sensu lato* and other closely related pinnotherids. Polyphyly of *Pinnixa s.l.* was confirmed by maximum likelihood analyses. By our restricted definition, the genus *Pinnixa sensu stricto* is represented in these analyses only by its type species, *Pinnixa cylindrica* (Say, 1818). As a result of these molecular analyses, in combination with morphological studies, twelve species are reassigned to existing genera: *Pinnixa faba* (Dana, 1851), *Pinnixa franciscana* Rathbun, 1918, *Pinnixa littoralis* Holmes, 1894, *Pinnixa schmitti* Rathbun, 1918, and *Pinnixa tubicola* Holmes, 1894 are placed in the genus *Scleroplax* Rathbun, 1893, whereas *Laminapinnixa miamiensis* McDermott, 2014, *Laminapinnixa faxoni* (Rathbun, 1918), *Pinnixa abbotti* Glassell, 1935, *Pinnixa arenicola* Rathbun, 1922, *Pinnixa floridana* Rathbun, 1918, *Pinnixa leptosynaptae* Wass, 1968 and *Laminapinnixa vanderhorsti* Rathbun, 1924 are reassigned to *Glassella* Campos & Wicksten, 1997, the last two strictly on morphological bases. In addition, three new genera are erected to receive nine species: *Rathbunixa* n. gen. includes members of the *Pinnixa pearsei* Wass, 1955 – *Pinnixa sayana* Stimpson, 1860 complex, *Pinnixa affinis* Rathbun, 1918, and species in the *Pinnixa californiensis* Rathbun, 1894 – *Pinnixa occidentalis* Rathbun, 1893 complex; *Tubicolixa* n. gen. includes *Pinnixa chaetopterana* Stimpson, 1860 and the *Pinnixa brevipollex* Rathbun, 1898 – *Pinnixa rapax* Bouvier, 1917 complex; and *Sayixa* n. gen. is established for *Pinnixa monodactyla* (Say, 1818).

KEY WORDS
Crab,
cryptic species,
Glassella,
Indopinnixa,
Laminapinnixa,
Rathbunixa,
Sayixa,
Scleroplax,
symbiotic,
Tubicolixa,
new genera,
new combinations.

RÉSUMÉ
Phylogénie du genre Pinnixa *White, 1846 (Crustacea, Brachyura, Pinnotheridae) et proches déduits de marqueurs moléculaires mitochondriaux et nucléaires, avec réaffectation générique de vingt-et-une espèces.*
Pour étudier les relations phylogénétiques entre les espèces de *Pinnixa* White, 1846 *sensu lato* et d'autres pinnotheridés étroitement apparentées, nous avons reconstruit une phylogénie moléculaire sur la base du complexe mitochondrial 16S-NADH1, du 12S mitochondrial et de l'histone 3 nucléaire. La polyphylie de *Pinnixa s.l.* a été confirmée par des analyses en maximum de vraisemblance. Selon notre définition restreinte, le genre *Pinnixa sensu stricto* n'est représenté dans ces analyses que par son espèce type, *Pinnixa cylindrica* (Say, 1818). Sur la base de ces analyses moléculaires, en combinaison avec des études morphologiques, douze espèces sont réaffectées à des genres existants : *Pinnixa faba* (Dana, 1851), *Pinnixa franciscana* Rathbun, 1918, *Pinnixa littoralis* Holmes, 1894, *Pinnixa schmitti* Rathbun, 1918 et *Pinnixa tubicola* Holmes, 1894 sont placées dans le genre *Scleroplax* Rathbun, 1893. *Laminapinnixa miamiensis* McDermott, 2014, *Laminapinnixa faxoni* (Rathbun, 1918), *Pinnixa abbotti* Glassell, 1935, *Pinnixa arenicola* Rathbun, 1922, *Pinnixa floridana* Rathbun, 1918, *Pinnixa leptosynaptae* Wass, 1955 et *Laminapinnixa vanderhorsti* (Rathbun, 1924) sont réaffectés à *Glassella* Campos & Wicksten, 1997, les deux derniers strictement sur des bases morphologiques. De plus, trois nouveaux genres sont érigés pour recevoir neuf espèces : *Rathbunixa* n. gen. comprend les membres du complexe *Pinnixa pearsei* Wass, 1955 – *Pinnixa sayana* Stimpson, 1860, *Pinnixa affinis* Rathbun, 1898 et des espèces du complexe *Pinnixa californiensis* Rathbun, 1894 – *Pinnixa occidentalis* Rathbun, 1893 ; *Tubicolixa* n. gen. est érigé pour recevoir *Pinnixa chaetopterana* Stimpson, 1860 et le *Pinnixa brevipollex* Rathbun, 1898 – complexe *Pinnixa rapax* Bouvier, 1917 – ; et *Sayixa* n. gen. représente une nouvelle combinaison pour *Pinnixa monodactyla* (Say, 1818).

MOTS CLÉS
Crabe,
espèces cryptique,
Glassella,
Indopinnixa,
Laminapinnixa,
Rathbunixa,
Sayixa,
Scleroplax,
symbiotique,
Tubicolixa,
genres nouveaux,
combinaisons nouvelles.

INTRODUCTION

Pinnixa White, 1846 is a long-standing pinnotherid genus, second in history only to the type genus of the family, *Pinnotheres* Bosc, 1802. As currently regarded, *Pinnixa sensu lato* (*s.l.*) is comprised of 51 species (the 50 species listed in the supplementary material of Palacios Theil *et al.* (2016) with the addition of *P. hendrickxi* Salgado-Barragán, 2015), which makes it also the second largest genus of the Pinnotheridae De Haan, 1833. Most of the species are from North to South American coasts, both Atlantic and Pacific, including the Gulf of Mexico and the Caribbean Sea. Six are, however, found in Indo-Pacific waters, with the distribution for one of them, *Pinnixa penultipedalis* Stimpson, 1858, reportedly reaching from Siberia to as far as the coasts of Mozambique (Schmitt *et al.* 1973). The genus has undergone partial revisions in recent decades resulting in reassignment of some species and descriptions of new genera (Manning & Felder 1989; Campos & Wicksten 1997; Ng & Naruse 2009; McDermott 2014; Palacios Theil *et al.* 2016), but it has never been subjected to comprehensive revision. About a third of the species within *Pinnixa s.l.* were described in the 19th century and more than half in the early 20th century, primarily in the course of studies based on museum materials. Most of these were collected during exploratory expeditions, especially along American coasts, as for example during the Albatross campaigns and similar efforts (Rathbun 1894, 1898; Glassell 1935a, b). It is likely that these species were placed in *Pinnixa s.l.* because of their sharing a consistently much-wider-than-long carapace and a third ambulatory leg longer than the others. However, these characters are probably not synapomorphies but rather convergent adaptations to a symbiotic life within elongated habitats such as the tubes of polychaete worms, burrows of sipunculans, burrows of infaunal decapods, or the cloacal lumens of holothurians.

Preliminary molecular analyses have indicated that *Pinnixa s.l.* is polyphyletic in its present composition on the basis of the mitochondrial complex formed by part of the 16S gene, the tRNA-Leu, and part of the gene for NADH dehydrogenase subunit I (Cuesta *et al.* 2002; Palacios Theil *et al.* 2009). However, the number of species included in those molecular phylogenetic revisions was very limited. Here we increase the number of taxa analyzed, while adding another mitochondrial gene (12S) and the nuclear gene for histone subunit 3 (H3). On this basis we reexamine phylogenetic associations among species of *Pinnixa s.l.*, as well as their relationships to other pinnotherid genera. Of special interest are the relationships of *Pinnixa s.l.* to other taxa within the subfamily Pinnixinae Števčić, 2005, such as *Austinixa* Heard and Manning, 1997, *Glassella* Campos and Wicksten, 1997, *Laminapinnixa* McDermott, 2014, and *Scleroplax* Campos, 2006, or to *Indopinnixa* Manning & Morton, 1987, which has not been included in previous phylogenetic analyses.

MATERIAL AND METHODS

Specimens in phylogenetic analyses

Phylogenetic analyses included samples of *Pinnixa s.l.* from both the western Atlantic and eastern Pacific coastlines of the Americas, representing all present and putative congeners available to us. To assess polyphyly of the genus *Pinnixa* and

clarify its phylogenetic relationships to other pinnotherid genera, samples of other pinnotherid taxa available as sequence quality materials were included in phylogenetic analyses using a concatenated alignment based on three fragments (Table 1). Representative species of the families Gecarcinidae MacLeay, 1838, Grapsidae MacLeay, 1838, Ocypodidae Rafinesque, 1815, Sesarmidae Dana, 1851, and Varunidae H. Milne Edwards, 1853 were used as outgroups.

DNA extraction, amplification, and sequencing

When specimens were large enough, the carapace was lifted at the posterior edge in order to obtain thoracic muscle tissue used for DNA extraction. Sometimes gills were also used but only after careful examination to rule out the presence of crustacean parasites. Total genomic DNA was extracted using the DNeasy Blood and Tissue Kit (QIAGEN, Valencia, CA, USA) or a standard DNA extraction protocol (Robles *et al.* 2007). Diluted total DNA was amplified by means of a polymerase chain reaction (PCR) following the recommendations of the Taq polymerase's manufacturers (AmpliTaq Gold® DNA Polymerase, Applied Biosystems, Foster City, CA, USA; M0273S Taq DNA Polymerase, New England BioLabs, Ipswich, MA USA; or DreamTaqTM Green DNA Polymerase, Fermentas, currently ThermoFisher Scientific, Waltham, MA, USA) in a Stratagene® Robocycler® Gradient 96 (Santa Clara, CA, USA). Three fragments were targeted: 1) a mitochondrial complex of about 830 bp consisting of part of the 16S rRNA gene, the tRNA-Leu, and part of the gene for NADH dehydrogenase subunit 1 (NADH1), 2) part of the mitochondrial 12S rRNA gene, and 3) part of the nuclear histone subunit 3 gene. These genes represent a diverse group of mitochondrial protein- or RNA-coding genes, as well as a nuclear protein-coding gene. They have been previously shown to be informative and have an adequate resolution to solve phylogenetic relationships between and among species and genera within Pinnotheridae (Palacios Theil *et al.* 2016; Tsang *et al.* 2018). In addition, they have proved to be obtained with relative ease using the primers indicated in Table 2, which shows also the length of the fragments obtained with each primer combination. PCR products were either sent to be purified and sequenced by Beckman Coulter Genomics (Danvers, MA, USA) or purified using SureClean (Bioline, Taunton, MA, USA), resuspended in water, sequenced with the ABI BigDye terminator mix, sequencing products being run on a 3100 Applied Biosystems (Foster City, CA, USA) automated sequencer.

Molecular analyses

The obtained sequences were assembled and manually edited when necessary with the program Sequencher 5.0 (Gene Codes, Ann Arbor, MI, USA). Preliminary alignments were assembled with BioEdit 7.1.3.0 (Hall 1999) and subsequently tested for accuracy with MAFFT (Multiple Alignment using Fast Fourier Transform, Katoh *et al.* 2002) on the website of the European Bioinformatics Institute (www.ebi.ac.uk, last visited 12th Oct 2018). Poorly aligned positions were identified with Gblocks v. 0.91b (Castresana 2000) on the server of the Mediterranean Center for Marine and Environmental Research (CMIMA, molevol.cmima.csic.es/castresana/ Gblocks.html, last visited 12th Oct 2018). As a result, 87% of the positions were used for the 16S-NADH1 fragment, and 86% of the original positions for 12S. For histone 3 no Gblocks analysis was necessary and the whole fragment could be used. The three resulting alignments were concatenated for more accuracy in the analyses (Gadagkar *et al.* 2005). Total sequence length was 1445 bp, as a result of concatenating 776 bp from the 16S-NADH1 fragment, 340 bp from 12S, and 327 bp from the histone 3 gene. For the 16S-NADH1 fragment 593 bp corresponded to the 16S rRNA gene, 68 bp to the gene for tRNA-Leu, and 98 bp to the gene for NADH1, with a fragment of 14 bp corresponding to an intron located between the tRNA-Leu and the NADH1 genes.

The alignment was submitted to the Cyberinfrastructure for Phylogenetic Research (CIPRES) web portal (www.phylo.org, last visited 12th Oct 2018) for Randomized Accelerated Maximum Likelihood (RAxML-HPC2 on XSEDE) analysis (version 8.2.8, Stamakis 2014) with 1000 bootstraps, the maximum number of bootstraps allowed by the tool, and supplying the information for the partition, which included six fragments: the 16S rRNA gene (1-593 bp), the gene for tRNA-Leu (594-662 bp), a fragment corresponding to an intron (663-677 bp), the gene for NADH1 (678-776 bp), the 12S rRNA gene (777-1117 bp), and the histone 3 gene (1118-1445 bp). The analysis showed that GTR was the best nucleotide substitution model for all fragments. This model was subsequently applied for a Bayesian phylogenetic analysis, performed using MrBayes on XSEDE also on the CIPRES web portal (Ronquist *et al.* 2011). The analysis was run with four Markov chains for 10 000 000 generations, sampling one tree every 1000 generations and with the burn-in percentage set to 25% of the samples. The resulting trees were analyzed and edited with Mega 5.2 (Tamura *et al.* 2011). The sequences and the complete alignments were submitted to GenBank for public access (Table 1). The majority of the sequences, those with GenBank accession numbers starting with EU and KU, had been made available by us as a result of previous publications (Palacios Theil *et al.* 2009, 2016), whereas the sequences with accession numbers starting with MN have been used here for the first time.

Morphological examination and illustration

The specimens were examined under a Wild Heerbrugg dissecting scope, and selected characteristic parts illustrated with the aid of a Leica *camera lucida*. Smaller parts were examined under an Olympus BH2 compound microscope and a Nikon inverted compound microscope. Hand drawings were scanned and thereafter edited with the graphic design software programs Adobe Illustrator® and Adobe Photoshop® (Adobe Systems, San Jose, CA, USA). In some instances, previously published line illustrations were adapted for use, provided they were public domain or allowed by special permission. Measurements, where reported, were rounded to the nearest 0.1 mm.

TABLE 1. — Pinnotherid specimens used in phylogenetic analyses of the genus *Pinnixa* White, 1846 *s.l.* and allies. Names shown are in accord with *Pinnixa s.l.* prior to revisions in present paper. See "Material and Methods" for museum abbreviations.

			GenBank Accession No.		
Species	**Collection locality**	**Collection No.**	**16S/tRNA-Leu/ND1**	**12S**	**Histone 3**
Subfamily Pinnixinae Števčić, 2005					
Austinixa aidae (Righi, 1967)	Praia Perequê Açú, Ubatuba, Brazil	ULLZ 5538	EU934966	KU679464	KU679742
Austinixa behreae (Manning & Felder, 1989)	Horn Island, West end, MS, USA	ULLZ 12942	KU679700	KU679470	KU679748
Austinixa chacei (Wass, 1955)	Horn Island, East end, MS, USA	ULLZ 14840	KU679702	KU679479	KU679757
Austinixa cristata (Rathbun, 1900)	Isle of Palms, SC, USA	ULLZ 4258	KU679681	KU679480	KU679758
Austinixa felipensis (Glassell, 1935)	San Felipe, Mexico	ULLZ 5558	EU934969	KU679484	KU679762
Austinixa gorei (Manning & Felder, 1989)	Islas del Rosario, Colombia	ULLZ 5586	EU934965	KU679486	KU679764
Austinixa patagoniensis (Rathbun, 1918)	Praia Dura, Ubatuba, Brazil	ULLZ 5550	KU679689	KU679490	KU679768
Glassella costaricana (Wicksten, 1982)	Isla Grande, Panama	ULLZ 14135	KU679660	KU679519	KU679794
	San Juanillo, Guanacaste, Costa Rica	ULLZ 15094	KU679659	KU679520	KU679795
Indopinnixa kumejima Naruse & Maenoso, 2012	Iguma Bay, Hahajima, Japan	ULLZ 17350	MN341021	MN341017	MN341030
Indopinnixa moosai Rahayu & Ng, 2010	Lombok, Indonesia	ZRC 2010.0099	MN341020	MN341018	MN341031
Laminapinnixa faxoni (Rathbun, 1918)	Isla Margarita, Venezuela	ULLZ 5567	KU679666	KU679523	KU679798
Laminapinnixa miamiensis McDermott, 2014	Fort Pierce, FL, USA	MNHN-IU-2017-9363	KU679663	KU679524	KU679799
Laminapinnixa miamiensis	Bocas del Toro, Panama	ULLZ 13338	KU679665	KU679526	KU679801
Pinnixa abbotti Glassell, 1935	Bahía de los Ángeles, Mexico	ULLZ 5618	KU679667	KU679535	KU679810
Pinnixa affinis Rathbun, 1898	Panama Canal entrance, Pacific	UF 18955	KU679721	KU679536	KU679811
Pinnixa arenicola Rathbun, 1922	Pos Chiquito, Aruba, Dutch Antilles	ULLZ 6070	KU679668	KU679537	KU679812
	Fort Pierce, FL, USA	ULLZ 9248	KU679669	KU679538	KU679813
	St. Martin, French Antilles	UF 32047	KU679670	KU679539	KU679814
	Carrie Bow Cay, Belize	ULLZ 16556	MN341022	MN341016	MN341026
Pinnixa chaetopterana Stimpson, 1860	Fort Pierce, FL, USA	ULLZ 5620	EU934962	KU679541	KU679816
	Beaufort, NC, USA	ULLZ 5737	KU679711	KU679542	KU679817
	Tampa Bay, FL, USA	ULLZ 8126	EU934960	KU679543	KU679818
	Carrie Bow Cay, Belize	ULLZ 12537	KU679708		KU679819
	St. Joseph Peninsula, FL, USA	ULLZ 12673	KU679713	KU679544	KU679820
	Choctawhatchee Bay, FL, USA	ULLZ 14640	KU679712	KU679545	KU679821
	St. Andrews Bay, FL, USA	ULLZ 14825	KU679714	KU679546	KU679822
	Isla Margarita, Venezuela	ULLZ 14079	KU679709	KU679547	KU679823
	Isla Margarita, Venezuela	ULLZ 14102	KU679710	KU679548	KU679824
Pinnixa cylindrica (Say, 1818)	Corpus Christi, TX, USA	ULLZ 5560	EU934963	KU679549	KU679825
	Harkers Island, NC, USA	MNHN-IU-2017-9365	KU679692	KU679550	KU679826
	Marco Island, FL, USA	ULLZ 12190	KU679690	KU679551	KU679827
	St. Joseph Peninsula, FL, USA	ULLZ 12675	KU679693	KU679552	KU679828
	off Perdido Key Beach, FL, USA	ULLZ 14832	KU679694	KU679554	KU679830
Pinnixa faba (Dana, 1851)	Washingston State, USA	ULLZ 5571	EU934976	KU679555	KU679831
Pinnixa floridana Rathbun, 1918	St. Joseph Peninsula, FL, USA	ULLZ 13102	KU679661	KU679556	KU679832
	Fort Pierce, FL, USA	ULLZ 13120	KU679662	KU679557	KU679833
Pinnixa franciscana Rathbun, 1918	Bodega Bay, CA, USA	ULLZ 5624	EU934974	KU679558	KU679834
Pinnixa littoralis Holmes, 1894	Tahuya, WA, USA	ULLZ 5572	EU934975	KU679559	KU679835
Pinnixa monodactyla (Say, 1818)	Fort Pierce, FL, USA	ULLZ 8713	MN341023	MN341014	MN341027
Pinnixa occidentalis Rathbun, 1893	Panama Canal entrance, Pacific	UF 18929	KU679722	KU679561	KU679837
Pinnixa pearsei Wass, 1955	Fort Pierce, FL, USA	ULLZ 5557	EU934971	KU679562	KU679838
	Marco Island, FL, USA	ULLZ 12188	KU679716	KU679563	KU679839
	Gulf Shores, AL, USA	ULLZ 14026	KU679715	KU679564	KU679840
Pinnixa rapax Bouvier, 1917	Praia do Araça, São Sebastião, Brazil	ULLZ 5568	EU934959	KU679567	KU679843
Pinnixa sayana Stimpson, 1860	Tampa, FL, USA	ULLZ 14029	KU679720	KU679571	KU679847
	Fort Pierce, FL, USA	ULLZ 14032	KU679717	KU679572	KU679848
	Corpus Christi, TX, USA	TCWC 2-3632	KU679719	KU679573	KU679849
Pinnixa scamit (?) Martin & Zmarzly, 1994	Brown Island, WA, USA	UF 11969	MN341024	MN341015	MN341029
Pinnixa schmitti Rathbun, 1918	Japonski Island, AK, USA	ULLZ 5574	EU934978	KU679574	KU679850
Pinnixa tubicola Holmes, 1894	Baranof Island, AK, USA	ULLZ 5621	EU934973	KU679577	KU679853
Pinnixa sp.	Bocas del Toro, Panama	ULLZ 13337	MN341025	MN341019	MN341028
	Isla Grande, Panama	ULLZ 14141	KU679671	KU679580	KU679856
Scleroplax granulata Rathbun, 1894	Bodega Bay, CA, USA	ULLZ 5576	EU934972	KU679590	KU679866
pinnotherid sp.	Bahía de los Ángeles, Mexico	ULLZ 9337	KU679732	KU679620	KU679896
Subfamily Pinnixulalinae Palacios Theil, Cuesta & Felder 2016					
Pinnixulala petersi (?) (Bott, 1955)	07°24.4'N, 80°13.7'W, off Panama, Pacific	ULLZ 13992	KU679640	KU679566	KU679842
Pinnixulala retinens (Rathbun, 1918)	Fort Pierce, FL, USA	ULLZ 9347	EU934992	KU679569	KU679845
Pinnixulala valerii (Rathbun, 1931)	Estero Coriento, Nicaragua	ULLZ 9336	EU934993	KU679578	KU679854
Pinnixulala sp.	28°30.02'N, 90°42.54'W, NGMx	ULLZ 5582	EU934991	KU679581	KU679857

TABLE 1. — Continuation.

Species	Collection locality	Collection No.	GenBank Accession No. 16S/tRNA-Leu/ND1	12S	Histone 3
Subfamily Pinnotherinae De Haan, 1833					
Afropinnotheres monodi Manning, 1993	Ria Formosa, Portugal	ULLZ 12029	KU679625	KU679462	KU679740
Alain raymondi Ahyong & Ng, 2008	09°26.9'N, 123°34.5'E, Philippines	ZRC 2008.0565	KU679636	KU679463	KU679741
Austinotheres angelicus (Lockington, 1877)	San Felipe, Mexico	ULLZ 9601	EU935002	KU679500	KU679778
Calyptraeotheres garthi (Fenucci, 1975)	Golfo San Matías, Argentina	ULLZ 14265	KU679652	KU679501	KU679779
Calyptraeotheres granti (Glassell, 1933)	San Felipe, Mexico	ULLZ 9599	EU934979	KU679502	KU679780
Clypeasterophilus juvenilis (Bouvier, 1917)	29°43.08'N, 85°53.16'W, NGMx	ULLZ 8566	KU679645	KU679503	
Clypeasterophilus rugatus (Bouvier, 1917)	East coast, FL, USA	ULLZ 5546	EU934980	KU679504	KU679781
Clypeasterophilus stebbingi (Rathbun, 1918)	Isla Margarita, Venezuela	ULLZ 5545	EU934983	KU679508	KU679784
Dissodactylus crinitichelis Moreira, 1901	Ilha Anchieta, Ubatuba, Brazil	ULLZ 5561	EU934982	KU679511	KU679787
Dissodactylus latus Griffith, 1987	East coast, FL, USA	ULLZ 5548	EU934985	KU679513	KU679789
Dissodactylus mellitae (Rathbun, 1900)	St. Joseph Peninsula, FL, USA	ULLZ 12715	KU679651	KU679514	KU679790
Fabia obtusidentata (Dai, Feng, Song & Chen, 1980)	Pattani, Thailand	ZRC 2003.0628	KU679723	KU679517	KU679792
Fabia subquadrata Dana, 1851	Bodega Bay, CA, USA	ULLZ 5575	EU935000	KU679518	KU679793
Holothuriophilus pacificus (Poeppig, 1836)	Cocholgue, Chile	ULLZ 5569	EU934997	KU679521	KU679796
Juxtafabia muliniarum (Rathbun, 1918)	San Felipe, Mexico	ULLZ 9600	EU934990	KU679522	KU679797
Limotheres nasatus Holthuis, 1975	off SC, USA	ULLZ 9176	EU934996	KU679527	KU679802
Nepinnotheres novaezelandiae (Filhol, 1885)	Oriental Bay, Wellington, New Zealand	AM P92429	KU679727	KU679528	KU679803
Nepinnotheres pinnotheres (Linnaeus, 1758)	Mediterranean, Spain	CBR-ICM 59/1992 586-A	EU935001	KU679529	KU679804
Orthotheres barbatus (Desbonne, 1867)	Los Roques, Venezuela	ULLZ 5559	EU934999	KU679530	KU679805
Pinnaxodes chilensis (H. Milne Edwards, 1837)	Cocholgue, Chile	ULLZ 5570	EU934998	KU679534	KU679809
Pinnotheres pisum (Linnaeus, 1767)	Germany, within imported oyster	SMF 30947	KU679725	KU679587	KU679863
Solenotheres prolixus Ng & Ngo 2010	Vinh Chan, Vietnam	ZRC 2010.0265	KU679726	KU679591	KU679867
Tumidotheres maculatus (Say, 1818)	Charleston Harbor, SC, USA	ULLZ 5508	KU679634	KU679596	KU679872
Tumidotheres margarita (Smith, 1869)	Magdalena Bay, Mexico	ULLZ 5533	EU934987	KU679601	KU679877
Tunicotheres moseri (Rathbun, 1918)	Tampa Bay, FL, USA	ULLZ 4516	EU934988	KU679606	KU679882
	Isla Margarita, Venezuela	ULLZ 5536	EU934989	KU679607	KU679883
Zaops ostreus (Say, 1817)	Delaware Bay, NJ, USA	ULLZ 13193	KU679658	KU679617	KU679893

ABBREVIATIONS

Collections

aM	Australian Museum, Sidney;
CBR-ICM	Colección Biológica de Referencia, Instituto de Ciencias del Mar, Barcelona;
NCBN-ZMA	Zoölogisch Museum Amsterdam, merged since 2001 into the Nederlands Centrum voor Biodiversiteit Naturalis, Amsterdam;
MNHN	Muséum national d'histoire naturelle, Paris;
SMF	Senckenberg Museum, Frankfurt;
TCWC	Texas Cooperative Wildlife Collection, currently the Biodiversity Research and Teaching Collection, Texas A&M University;
UF	Florida Museum of Natural History, University of Florida, Invertebrate Zoology Collection, Gainesville;
ULLZ	University of Louisiana at Lafayette Zoological Collection, Lafayette;
ZRC	Zoological Reference Collection of the Raffles Museum of Biodiversity Research, National University of Singapore.

Unless otherwise indicated in parentheses, each catalog number represented a single specimen.

Locations

States of the USA are abbreviated with two upper case letters, countries with three upper case letters, and specific localities with combinations of upper and lower case letters. For Costa Rica, Mexico and Panama, a "P" after the country abbreviation indicates the sample was collected at the Pacific coast of that country, as opposed to in the Caribbean. Abbreviations as follows:

AK	Alaska;
AL	Alabama;
ARU	Aruba;
BEL	Belize;
Boc	Bocas del Toro, Panama;
BRA	Brazil;
CA	California;
Cha	Chactawhatchee Bay, FL, USA;
CRI P	Costa Rica, Pacific coast;
FL	Florida, USA;
Ft P	Fort Pierce, FL, USA;
IND	Indonesia;
Is G	Isla Grande, Panama;
JAP	Japan;
M Is	Marco Island, FL, USA;
MEX P	Mexico, Pacific coast;
NC	North Carolina;
NGMx	northern Gulf of Mexico;
PAN P	Panama, Pacific coast;
Per K	Perdido Key, FL, USA;
St A	Saint Andrew Bay, FL, USA;
St J	Saint Joseph Bay, FL, USA;
St M	Saint Martin, French Antilles;
Tam	Tampa Bay, FL, USA;
TX	Texas;
USA	United States of America;
VEN	Venezuela;
WA	Washington.

TABLE 2. — Primers used in this study. The length of the fragments obtained is approximate for pinnotherids, without trimming. References: **1**, Crandall & Fitzpatrick Jr. 1996; **2**, Schubart *et al.* 2001; **3**, Palacios Theil *et al.* 2009; **4**, Schubart 2009; **5**, Buhay *et al.* 2007; **6**, Svenson & Whiting 2004.

gene	primer	sequence in 5' to 3' direction	references	primer pair	bp obtained
16S rDNA	1472	AGA TAG AAA CCA ACC TGG	1	16S-L2	580
	16S-L2	TGC CTG TTT ATC AAA AAC AT	2	1472	580
	16S-pH1	CGC TGT TAT CCC TAA AGT AAC	3	16S-L2	415
	16S-pH2	CCT GGC TCA CGC CGG TCT GAA	3	16S-L2	570
				16S-pL1	380
	16S-pH3	AAT CCT TTC GTA CTA AAA	3	16S-pL1	430
	16S-pL1	AAC TTT TAA GTG AAA AGG CTT	3	16S-pH2	380
				16S-pH3	430
	16S-pL2	TTA CTT TAG GGA TAA CAG CG	3	NADH1	465
ND1 + tRNA-Leu	16S-L6	TTG CGA CCT CGA TGT TGA AT	3, 4	NADH1	410
	NADH1	TCC CTT ACG AAT TTG AAT ATA TCC	3, 4	16S-L6	410
				16S-pL2	465
12S rDNA	12Sf	GAA ACC AGG ATT AGA TAC CC	5	12S1R	395
	12S1R	AGC GAC GGG CGA TAT GTA C	5	12Sf	395
Histone 3	HexAF	ATG GCT CGT ACC AAG CAG ACG GC	6	HexAR	375
	HexAR	ATA TCC TTG GGC ATG ATG GTG AC	6	HexAF	375

Morphology

P pereopod;
cl carapace length;
cw carapace width.

RESULTS

GENETIC ANALYSES

DNA extraction and sequencing were successful for all the specimens of *Pinnixa* included in the analyses, with the exception of the 12S sequence for *Pinnixa chaetopterana* Stimpson, 1860 (ULLZ 12537). This sequence was obtained only after repeated attempts and was not of good quality, probably due to the presence of multiple fragments of similar size, possibly indicating pseudogenes or contamination. About 10% of the positions in the obtained fragment were ambiguous, and the sequence was about 80% similar to other 12S sequences of *P. chaetopterana*, a species to which it was thought to be related based on morphology. For pinnotherids, the similarity between 12S sequences from different specimens of the same species is higher than 95%. Only the 16S-NADH1 and histone 3 fragments for the problematic specimen were included in the analyses. Results related to this sample must therefore be interpreted with caution (Fig. 1). Attempts at obtaining the histone 3 sequence for *Pinnixa latissima* Coelho, 1997 (ULLZ 14136) were unsuccessful and for this sample only the 16S-NADH1 and 12S fragments were available. However, these fragments were of uncertain quality. In addition, no re-extractions could be performed without risking excessive damage to the only available specimen. For these reasons we chose to exclude this sample from the alignment.

Additional samples were available that could not be included in the analyses due to our inability to obtain sequences. In these cases, DNA extractions were of poor quality or yielded low concentrations, and, although PCRs were attempted repeatedly for different genes, they did not succeed. These included specimens of *Pinnixa cylindrica* (Say, 1818) (USNM 1192250), *Pinnixa latissima* (USNM 1192248), *Pinnixa leptosynaptae* Wass, 1968 (ULLZ 14834), and some specimens that belonged to the *Pinnixa faxoni* complex, probably representing the poorly defined *Laminapinnixa faxoni* (Rathbun, 1918) or *L. vanderhorsti* Rathbun, 1922 (ULLZ 4430 and USNM 1192261).

Among all the taxa included in the analyses, the species of *Pinnixulala* formed a clade separate from both the subfamily Pinnotherinae De Haan, 1833 and the subfamiliy Pinnixinae (Fig. 1). It included the species *Pinnixulala valerii* (Rathbun, 1931), the tentatively identified *Pinnixulala petersi* (?) (Bott, 1955), *Pinnixulala retinens* (Rathbun, 1918), and *Pinnixulala* sp., and none of the species of *Pinnixa*, or any other taxa which show a carapace wider than long, were closely allied to them.

The rest of the species within *Pinnixa s.l.* formed six subclades within the subfamily Pinnixinae. Five of the subclades formed a large clade, which included *Pinnixa cylindrica* (type of the genus *Pinnixa*), as well as *P. monodactyla* (Say, 1818); the *P. chaetopterana*, *P. sayana* and *Scleroplax* complexes (Fig. 1); and a subclade formed by those species of *Austinixa* included in the analysis. Support values for this clade were high (100/100). Within the clade, *P. monodactyla* separated from all other species at a basal node. Noteworthy were also the very small genetic distances observed among the included samples of *P. cylindrica*, even though these ranged from locations along the Atlantic and Gulf of Mexico coasts from North Carolina to Texas. The sixth subclade within subfamily Pinnixinae grouped some species of *Pinnixa* with *Glassella costaricana* Wicksten, 1982, *Indopinnixa kumejima* Naruse and Maenoso, 2012, *Indopinnixa moosai* Rahayu and Ng, 2010, *Laminapinnixa miamiensis* McDermott, 2014, and *L. faxoni* (Rathbun, 1918), forming the *Glassella-Indopinnixa* complex, with high support (95/100). It included the Atlantic species *P. arenicola* Rathbun, 1922, *P. floridana* Rathbun, 1918, *Pinnixa* sp., and the Pacific *P. abbotti* Glassell, 1935 (Fig. 1, *Glassella-Indopinnixa* complex). In addition to the aforementioned, an unidentified pinnotherid species from the Pacific coast of Mexico (ULLZ 9337), probably symbiotic with worms, also resolved within the subfamily Pinnixinae. It occupied a monotypic branch

FIG. 1. — Phylogeny for species of superfamily Pinnotheroidea De Haan, 1833, emphasis on genus *Pinnixa* White, 1846 *s.l.* inferred from Randomized Accelerated Maximum Likelihood (RAxML) analysis of a 1445 bp long fragment concatenated from the mitochondrial complex 16S/tRNA-Leu/ NADH1 (776 bp), the mitochondrial 12S rRNA gene (340 bp) and the nuclear gene for the histone 3 subunit (327 bp). Bootstrap support values are shown at the nodes when higher than 50%. Collection number follows the species name to identify samples. For samples in the subfamily Pinnixinae Števčić, 2005, abbreviations indicating geographic origin are defined in "Materials and Methods". Species name combinations as shown are prior to revisions in present paper. Abbreviations as in Material and Methods.

that separated from all other Pinnixinae at a basal node. The support values for the clade encompassing all of the species within the subfamily were high (88/99).

All species of *Pinnixa* from the Pacific coasts of the USA grouped with *Scleroplax granulata* Rathbun, 1894 at a high level of support (99/100). This included *P. faba* (Dana, 1851), *P. franciscana* Rathbun, 1918, *P. littoralis* Holmes, 1894, *P. schmitti* Rathbun, 1918, and *P. tubicola* Holmes, 1894, in addition to a juvenile specimen tentatively identified as *P. scamit* (?) Martin & Zmarzly, 1994. It was notable that genetic distances among the taxa included within this group were rather small when compared to the distances among species in other subclades (Fig. 1, *Scleroplax* complex).

The *Scleroplax* complex was a sister clade to the *P. sayana* complex, which was represented by a highly supported clade (100/100) composed of the Atlantic species *P. sayana* Stimpson, 1860 and *P. pearsei* Wass, 1955, along with the Pacific species *P. affinis* Rathbun, 1898 and *P. occidentalis* Rathbun, 1894. The samples morphologically identified as *P. pearsei* and *P. sayana* within this group did not separate into two subclades but instead formed one polyphyletic clade, with small genetic distances among the taxa included (Fig. 1, *P. sayana* complex).

Lastly, representatives of the western Atlantic species *P. chaetopterana* and *P. rapax* Bouvier, 1917 joined in a highly supported clade (100/100). Within this clade, *P. chaetopterana* and *P. rapax* grouped together, with no or low support (-/67) for the separation between *P. rapax* and the samples of *P. chaetopterana* from the different locations available. However, samples of *P. chaetopterana* from the Caribbean Sea (Venezuela and Belize) formed a highly supported subclade (98/99), as did the two samples from the northern reaches of the western Atlantic (North Carolina and Fort Pierce, Florida), although with lower support values (94/71). Four additional samples from the Gulf of Mexico also grouped together in topology, although this subclade showed significant support values only for the Bayesian analysis (-/92). The one sample of *P. rapax* was nested together with the Caribbean samples of *P. chaetopterana*, but again without significant support (-/67) (Fig. 1, *P. chaetopterana* complex).

In the *Glassella-Indopinnixa* complex all American species included in the analyses, with the exception of an undetermined species from Panama (ULLZ 13337 and ULLZ 14141), formed a highly supported group (100/100), including among others those species recently reassigned to the genus *Laminapinnixa* McDermott, 2014, as well as *Glassella costaricana*. This group appeared as a sister clade of the two Asian species analyzed (*Indopinnixa kumejima* and *I. moosai*). The undetermined Panamanian species separated from them at a basal node within the complex (Fig. 1, *Glassella-Indopinnixa* complex).

Morphological examinations

Morphology of the members of the six clades resolved in the molecular phylogenetic analyses was re-evaluated in order to reverse-engineer arrays of morphological characters that supported these clade separations. Most commonly, these characters were found to include features of the carapace, the robustness and setation of the pereopods, shape of the male pleon, and proportions of the third maxilliped segments (Fig. 2).

Most members of the *Glassella-Indopinnixa* complex could be readily separated from the other taxa within the subfamily Pinnixinae by, among other characters, morphology of the third maxilliped. Except for *Glassella costaricana*, they all showed a third maxilliped with a long palp, where the club-shaped dactylus was as long or nearly as long as the ischiomerus and with it inserted at the proximal end of a stout conical propodus. The dactylus and the propodus were oriented in a wide angle, sometimes almost perpendicular, to each other (Fig. 2H). In *Glassella costaricana* the dactylus was strongly reduced, and it inserted at the distal portion of the propodus (Fig. 2G). In all other taxa examined for the subfamily Pinnixinae the third maxilliped showed elongate dactylus and propodus, similar in shape and size to each other, reaching to or past half the length of the ischiomerus (Fig. 2C, L, P, T, X). Additionally, the nine species in the *Glassella-Indopinnixa* complex shared a smooth but punctate carapace, relatively stout legs with dactyli shorter than the propodi (especially for P4 and P5; Fig. 2E), and a setose, somewhat elongate cheliped with relatively straight fingers and one or more rows of tubercles or granules on the outer surface of the palm, running along its length, the inferior one usually continuing along the fixed finger (Fig. 2F). Within the *Glassella-Indopinnixa* complex, *Glassella costaricana*, *P. arenicola*, *P. abbotti*, *Indopinnixa kumejima*, and *I. moosai* were easily distinguishable from each other on the basis of key characters from descriptive literature, as were males of *Laminapinnixa miamiensis*, *L. faxoni*, and *P. floridana*, three species with partially overlapping distributions. The latter three species could be easily distinguished by the shape of their pleon and the relative development of a gonopodal plate. However, the females could be discriminated only by subtle differences in the relative length of the pereopods dactyli, sharpness of the ridge running along the anterolateral margins, numbers, and positions of teeth on the posterior margin of the third ambulatory leg (P4), relative setation of legs and carapace margins, or coloration of the carapace.

P. pearsei, *P. sayana*, *P. affinis*, and *P. occidentalis* were observed to share a carapace with defined regions and a sharp cardiac ridge, slender legs with a long slender merus, and smooth chelipeds with a strongly reduced or deflexed fixed finger. Their third maxilliped also had a club-shaped propodus and dactylus oriented nearly parallel to each other. (Fig. 2J-M). According to Wass (1955) the differences between *P. pearsei* and *P. sayana* are evident in a higher and straighter cardiac crest, a wider carapace, and a broader propodus of P4 in *P. pearsei*. However, we observed great variation in these characters, as well as in the morphology of the chelipeds (Fig. 3A-E). The size of the examined male specimen of *P. occidentalis* was smaller (cw = 7.25 mm, cl = 3.35 mm as opposed to cw = 9.5 mm, cl = 19.5 mm) and somewhat less granulate than indicated in the literature. However, carapace, legs, and especially the chelipeds, with a characteristic large blunt tooth on the margin of the fixed finger (Fig. 3F, with chela of *P. affinis* for comparison, Fig. 3G), matched the species description (Rathbun, 1894).

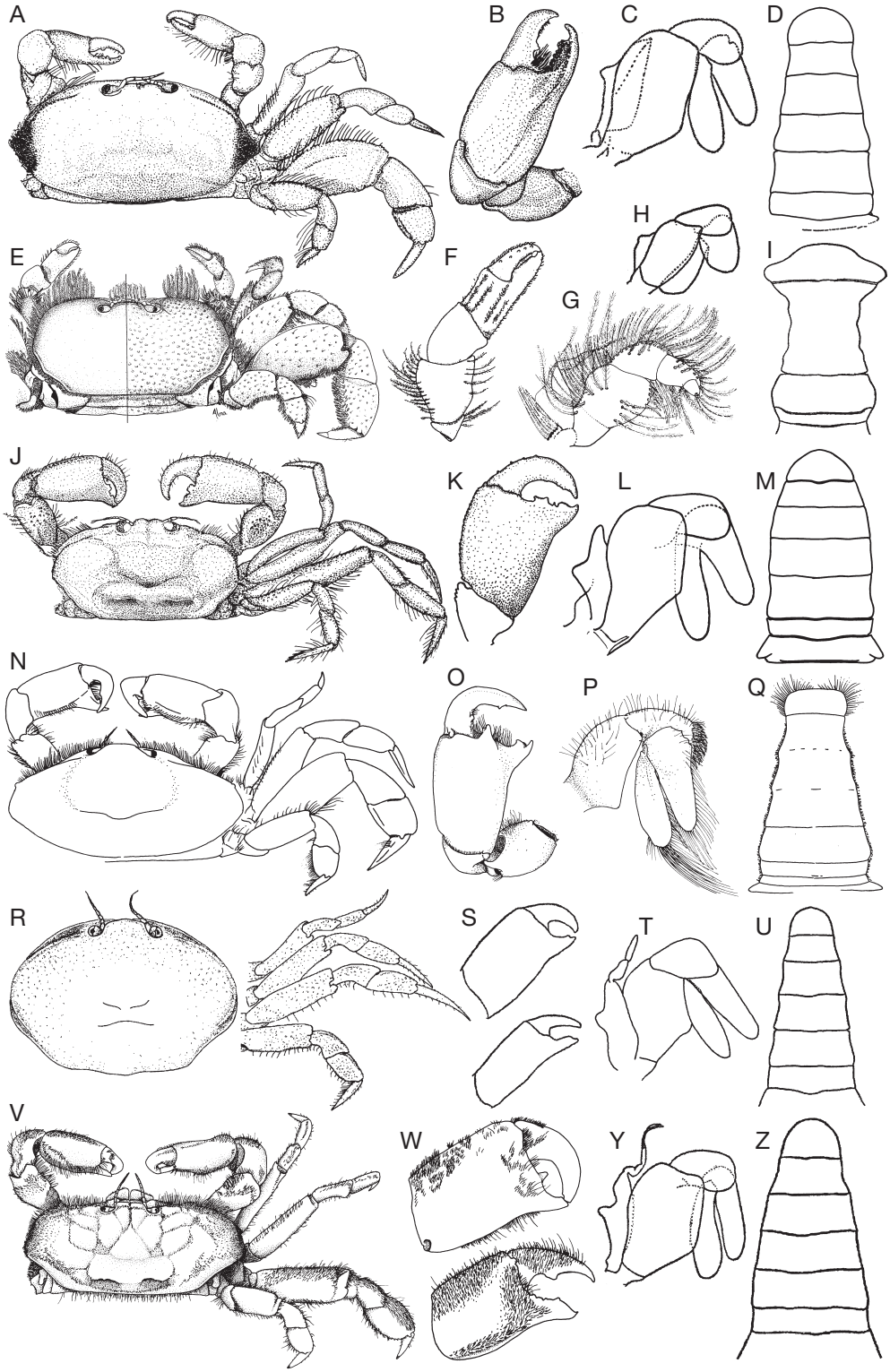

FIG. 2. — Morphological characters of the type species of *Pinnixa* White, 1846 *s.s.*, *P. cylindrica* (Say, 1818), along with those for five molecularly segregated genera formerly treated in *Pinnixa s.l.*: **A**-**D**, *Pinnixa cylindrica*: **A**, male dorsal view; **B**, male cheliped; **C**, third maxilliped (adapted from Rathbun 1918:160 fig. 99a); **D**, male pleon; **E**-**G**: *Glassella costaricana* (Wicksten, 1982): **E**, female holotype dorsal view; **F**, female cheliped; **G**, third maxilliped (adapted from Campos & Wicksten 1997: fig. 1, fig. 2c, a, with permission from Allen Press); **H**, **I**, *Glassella faxoni* (Rathbun, 1918) n. comb.: **H**, third maxilliped; **I**, male pleon (adapted from Rathbun 1918:133 fig. 77b, a); **J**-**M**: *Rathbunixa sayana* (Stimpson, 1960) n. comb.: **J**, male dorsal view; **K**, male cheliped; **L**, third maxilliped; **M**, male pleon (**L**, **M** adapted from Rathbun 1918:158 fig. 98a, b); **N**-**Q**: *Sayixa monodactyla* (Say, 1818) n. comb., male (ULLZ 8713, Fort Pierce, FL, USA); **N**, dorsal view; **O**, cheliped; **P**, third maxilliped; **Q**, pleon; **R**, **T**, **U**, *Scleroplax granulata* Rathbun, 1893; **R**, female carapace and pereopods 2-5; **T**, third maxilliped; **U**, male pleon (**R**, **T** adapted from Campos 2006:fig. 1a-c, with permission from Magnolia Press; **U**, adapted from Rathbun 1918:171 fig. 109a); **S**, *Scleroplax littoralis* (Holmes, 1894) n. comb., female and male chelipeds (adapted from Rathbun 1918:146 fig. 89a, b); **V**-**Y**, *Tubicolixa chaetopterana* (Stimpson, 1860) n. comb.: **V**, male dorsal view; **W**, female and male chelipeds; **X**, third maxilliped; **Y**, male pleon (**X**, **Y**, adapted from Rathbun 1918:152 fig. 94a, b).

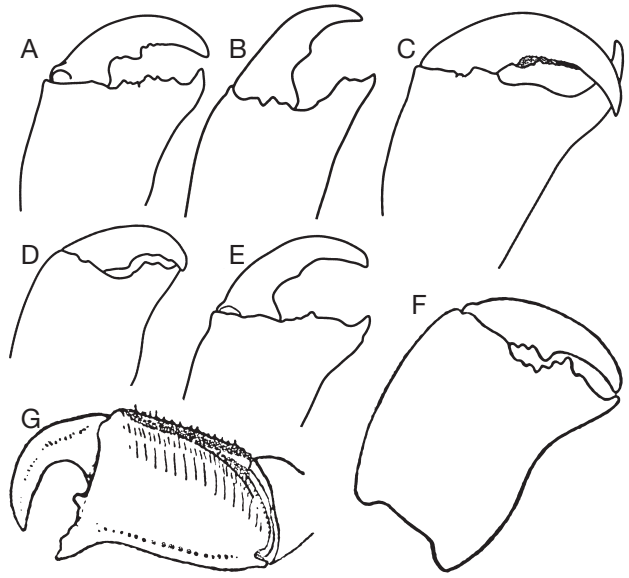

FIG. 3. — Variation in the chelae in *Rathbunixa* n. gen.: **A**-**E**: left cheliped, dorsal (inner) surface; **A**-**C**, *R. pearsei* (Wass, 1955) n. comb. female, ULLZ 5557 (**A**); ovigerous female, ULLZ 12188 (**B**); ovigerous female, ULLZ 14026 (**C**); **D**-**E**, *R. sayana* (Stimpson, 1960) n. comb.: female, ULLZ 14032 (**D**); ovigerous female, ULLZ 14029 (**E**); **F**, *R. occidentalis* (Rathbun, 1893) n. comb., left cheliped of male, USNM 17470 (adapted from Rathbun 1918:155, fig. 96); **G**, *R. affinis* (Rathbun, 1894) n. comb., 1898, right cheliped of female holotype, USNM 21594 (adapted from Rathbun 1918:168, fig. 106). Not to scale.

Besides the sample used for the molecular analyses (ULLZ 8713), undoubtedly identifiable as a male of *Pinnixa monodactyla*, the only other specimen of this species available to us was an immature female collected with a box dredge in the northern Gulf of Mexico from about 39 m deep (ULLZ 8569). Despite the differences in size, sex, and origin, they showed obvious similarities. They presented a characteristic cheliped palm with a fixed finger reduced to a sharp spine, with an additional tooth at the base of the cheliped dactylus, and an elongated carapace with a tubercle on each anterolateral angle. Ambulatory legs were slender, cylindrical, with slender straight dactyli (Fig. 2N-Q).

Species in the *Scleroplax* complex shared a hard convex carapace and a third maxilliped with both the propodus and carpus long and spatulate. With the exception of *P. scamit*, they all had cylindrical legs (Fig. 2R-U). Unlike the other species in the complex, the examined juvenile specimen of *P. scamit* had slender legs, similiar to those observed for *P. affinis* and other species included in the *P. sayana* complex. In the *Scleroplax* complex, morphology supported the similarity between *P. littoralis* and *P. faba*, as indicated by Zmarzly (1992). They could be distinguished from each other only by the geometry of the cheliped fingers. This was easily observed for males, but for females the differences were again rather subtle. In females of *P. littoralis* the fixed finger of the cheliped is "slightly deflexed", and a gape is visible when the fingers are closed, as opposed to a "nearly straight" fixed finger and no gape in *P. faba* (Zmarzly 1992).

The specimens of *P. chaetopterana* and *P. rapax* were similar in having a carapace with clearly delimited regions, and in the relatively strong and pubescent chelipeds with a shortened or deflexed fixed finger in males, the slender dactyli of the ambulatory legs, and concentrations of pubescence on the pereopods and carapace margins. Their third maxilliped had both the elongate propodus and dactylus of similar size and shape (Fig. 2V-Y). The geographically separated samples of *P. chaetopterana*, similar to observations for *P. pearsei* and *P. sayana*, show variability in the morphology of the chelipeds, as well as in the relative length of the articles of the ambulatory legs, especially the dactyli. In addition, there were differences in number and sharpness of the granules and teeth on the edge of the subbranchial region as well as on the posterior surface of the P4 merus. The specimen of *Pinnixa chaetoperana* from Belize (ULLZ 12537) was a small juvenile, similar to *P. chaetopterana* in appearance of a carapace with clearly defined regions and in the denticulate meri of the fourth and fifth pereopods. The cheliped was similar to the female chelipeds for *P. chaetopterana* (see Fig. 2W). On the other hand, it was not as setose as most other specimens of *P. chaetopterana*.

SYSTEMATICS

Family PINNOTHERIDAE De Haan, 1833
Subfamily PINNIXINAE Števčić, 2005

Genus *Glassella* Campos & Wicksten, 1997

Glassella Campos & Wicksten, 1997: 69.

TYPE SPECIES. — *Glassella costaricana* (Wicksten, 1982) [*Pinnixa*] assigned by monotypy when genus was erected (Campos & Wicksten 1997).

ORIGINAL DESCRIPTION BY CAMPOS & WICKSTEN (1997). — "Carapace suboblong, dorsal surface pockmarked, wider than long, integument firm, regions not defined; cardiac ridge lacking; front truncated, with shallow median sulcus. MXP3 [= third maxilliped] with ischium-merus pyriform, fused, separated by faint line and distal margin truncated; palp as long as ischium-merus, 3-segmented, dactylus small, digitiform, inserted sub-distally on inner face of conical propodus; carpus stout, longer than combined length of propodus and dactylus; exopod with median lobe on outer margin, flagellum 2-segmented. WLl-4 [= walking leg] pockmarked, relative length 3 > 2 > 1 > 4, WL3 considerably the longest. Abdomen of female with 6 somites and telson free, widest at third somite; tapering from fourth somite to triangular telson. Male unknown."

DIAGNOSIS. — (Modified from Campos & Wicksten 1997). Carapace transversely oblong, wider than long, dorsal surface smooth, punctate, integument firm, regions poorly defined, sometimes with blunt ridge across posterior portion of carapace, ridge not extending entirely across carapace. Third maxilliped with ischiomerus pyriform or subtrapezoidal, fused, sometimes separated by faint line; palp as long as or longer than ischiomerus, three-segmented; dactylus sometimes (*Glassella costaricana*) very small, inserting sub-distally on inner face of conical propodus, typically large, nearly as long as ischiomerus, inserting near base of propodus. Chelipeds small, subcylindrical to weakly compressed, setose; palm typically with one or more longitudinal ridges or lines of tubercles or setae on

outer surface; fingers slender, dactylus superior margin typically with row of long setae. Walking pereopod articles heavy, stout, often marginally tuberculate or dentate, relative lengths P4 > P3 ≥ P2 > P5. Male pleon terminally broad, lobate to weakly polygonal; third pleonal somite typically bearing gonopodal plate or sheath extending between or against gonopods (Fig. 2E-I). Male gonopods heavy, stout, terminally forming sharp angle, spinose tip, or distally to laterally directed corneous filament.

INCLUDED SPECIES. — *Glassella abbotti* (Glassell, 1935) n. comb. [*Pinnixa*];
Glassella arenicola (Rathbun, 1922) n. comb. [*Pinnixa*];
Glassella faxoni (Rathbun, 1918) n. comb. [*Laminapinnixa*];
Glassella floridana (Rathtbun, 1918) n. comb. [*Pinnixa*];
Glassella miamiensis (McDermott, 2014) n. comb. [*Laminapinnixa*];
Glassella leptosynaptae (Wass, 1968) n. comb. [*Pinnixa*];
Glassella vanderhorsti (Rathbun, 1922) n. comb. [*Laminapinnixa*].

MATERIAL EXAMINED. — In addition to the material included in the phylogenetic analyses (Table 1) the following samples were available for examination:
Glassella abbotti n. comb. — ULLZ 5619 (26), ULLZ 7392 (Bahía de los Ángeles, Mexico);
Glassella arenicola n. comb. — NCBN-ZMA De242240 (holotype, Spanish Harbor, Curaçao), ULLZ 6070 (Aruba); ULLZ 8989 (Puerto Rico), ULLZ 9248 (Ft. Pierce, FL, USA);
Glassella costaricana. — UF 18960 (Isla Culebra, Panama);
Glassella faxoni n. comb. — ULLZ 14837 (Campeche, Mexico), ULLZ 14030 (Isla Margarita, Venezuela), ULLZ 14098 (2) (Punta Elvira, Venezuela);
Glassella floridana n. comb. — ULLZ 5649, ULLZ 17733 (Fort Pierce, FL, USA), ULLZ 13888 (Content Keys, FL, USA), ULLZ 14903 (2) (Alligator Point, FL, USA), ULLZ 13096, ULLZ 14038 (4), ULLZ 14181, ULLZ 15010 (St. Joseph's Bay, FL, USA), ULLZ 17469 (northeastern Gulf of Mexico);
Glassella miamiensis n. comb. — ULLZ 5724, MNHN-IU-2017-9364 = former ULLZ 7398 (2), ULLZ 11709, ULLZ 13338, ULLZ 14003, ULLZ 14011, ULLZ 14138 (Fort Pierce, FL, USA);
Glassella leptosynaptae n. comb. — ULLZ 14834 (Florida Bay, FL, USA);
Glassella vanderhorsti n. comb. — NCBN-ZMA.C RUS.D 242234 (holotype, Spanish Harbor, Curaçao).

REMARKS

The morphological similarities among species transferred to this genus have in most cases been noted previously (Rathbun 1918, 1924; Glassell 1935a; McDermott 2014), although their resemblance to *Glassella* of Campos & Wicksten (1997) has likely remained unnoticed because of the weight given to differences in the third maxilliped (Fig. 2G, H), often an important character in pinnotherids. However, there are other cases among pinnotherid genera for which striking variation in the third maxilliped has been observed among closely related species. In *Calyptraeotheres* Campos, 1990 some species lack a third maxilliped dactylus, whereas in others it is present (Hernández-Ávila & Campos 2006).

The genus *Laminapinnixa* was erected by McDermott (2014) to accomodate *L. miamiensis*, a newly described species for populations that we and colleagues had long regarded on morphological evidence as closely related to *Glassella faxoni* n. comb. and *G. vanderhorsti* n. comb. The genus was diagnosed in part by the presence in males of a plate (therein termed "abdominal plate" = our gonopodal plate) derived from the pleon (posterior to the gonopods), which

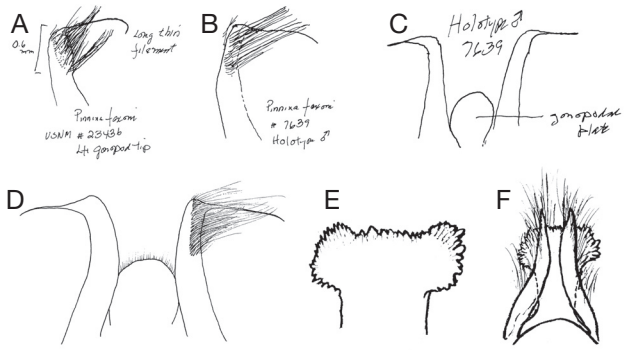

FIG. 4. — Reproduced thumbnail sketches of male gonopods and gonopodal plates on lost USNM specimens of *Glassella faxoni* (Rathbun, 1918) n. comb. (**A**-**C**), by R. H. Gore, 1978-1979; *G. faxoni* n. comb. (**D**), und *Glassella vanderhorsti* (Rathbun, 1922) n. comb.; (**E**, **F**) by D. L. Felder, 1979-1982. **A**, left gonopod, pleonal surface, paratype, USNM 23436; **B**, left gonopod, pleonal surface, holotype, USNM 7639; **C**, gonopods and gonopodal plate, pleonal surface, holotype USNM 7639; **D**, gonopods and gonopodal plate, pleonal surface, holotype, USNM 7639; **E**, gonopodal plate, pleonal surface, topotypic material, USNM 56903; **F**, gonopods and gonopodal plate, pleonal surface, topotypic material, USNM 56903.

in the description and discussion by McDermott (2014) are portrayed as a structure that must be "lifted" to expose the gonopods during copulation. However, this structure is in all unmanipulated examples of *G. miamiensis* n. comb. that we have examined positioned to extend from its more posterior origin obliquely between the gonopods (derived from the first pleonal somite) and then anterior to them, where it usually broadens terminally and separates the gonopods from the sternum when the pleon is flexed (as shown clearly by McDermott, 2014: fig. 7B). This would appear to not necessarily separate them from exposure for copulation when the pleon is extended (or, as they appear when illustrated with the pleon removed, Fig. 5F). The broadened terminus of the plate in at least one related species can also perhaps move from anterior or posterior of the gonopods, provided the gonopods are flexed laterally, though this seems unlikely in *G. miamiensis* n. comb.

In the course of describing and investigating potential relationships of *G. miamiensis* n. comb. and seeking evidence of other species having this gonopodal plate, McDermott (2014) noted the unfortunate loss of types for potentially related species to which he had wished to make comparisons. By way of further explanation, most of these were among 98 pinnotherid specimens permanently lost to science when destroyed by the U.S. Postal Service, owing to the mishandling of a loan return shipment by a borrower in 2006. While this loss has also limited our own comparative efforts, one of us (DLF) and his late colleague Robert H. Gore had independently examined types and other now lost materials decades ago, at the time making rough-sketches of selected structures, several of which are herewith directly reproduced given the void they fill (Fig. 4). In addition, high-quality, previously unpublished illustrations by several Smithsonian Institution illustrators, contracted by Robert Gore or the late Waldo Schmitt (the latter for a never-published manuscript by W. L. Schmitt

and E. S. Davidson), are in some cases annotated so as to be clearly identifiable with the now-lost types or other materials on which they were based (Fig. 5).

From this evidence, it is clear that both *G. faxoni* n. comb. and *G. vanderhorsti* have forms of the gonopodal plate in mature males that we regard to be homologs of that in *G. miamiensis*, in addition to their sharing a number of other characters that group them with *G. miamiensis* and its herewith assigned congeners. The illustrated male gonopodal plate for *Glassella vanderhorsti*, published by McDermott (2014) but reproduced here from the original figures with credit and voucher indicated (Fig. 5F), was in fact based on the Zoological Museum Amsterdam (now Naturalis Biodiversity Center, Netherlands) holotype male (NCBN-ZMA.C RUS.D 242234). In a very similar but smaller topotypic male specimen (USNM 56903), also collected by van der Horst but now among the lost materials, the gonopodal plate was found to be somewhat longer but terminally very similar to the holotype male and like that of *G. miamiensis* in that its terminal reaches were positioned anterior to the gonopods (Fig. 4E, F). Only in *G. faxoni* n. comb. was the male gonopodal plate found to be small enough to be positioned largely between the gonopods or to freely move its arched terminal lobe from anterior to posterior of the gonopods (Fig. 4C, D). As evident, the cataloged specimens upon which our figures, sketches, and notes are based were the same as examined by Rathbun (1918, 1924). This confirms personal communications of E. S. Davidson regarding gonopodal plates in these species, as were mentioned by McDermott (2014), who found the lack of Rathbun mentioning these plates in descriptions of *G. faxoni* n. comb. and *G. vanderhorsti* as reason to question their congeneric assignment with *G. miamiensis*. We suspect that Rathbun at the time attached little importance to gonopods as characters, especially among pinnotherids in the early years while she was working primarily with a hand-lens.

While the male gonopodal plate, or some ramification of it, may prove to unite most if not all species that we here assign to *Glassella*, our molecular phylogeny includes species in which it is at very least not reported to date, or for which intact male specimens are lacking. This remains the case for the generic type species, *G. costaricana*, known only from a female at the time of description. Our phylogenetic analyses included two additional females, but we also attempted inclusion of tissues from a very small mutilated male specimen (UF 18960) that appeared to be this species. Its identity as *G. costaricana* was confirmed by clear match of its 16S mitochondrial sequence to those of the females, but it was not included in the final phylogenetic analysis for lack of additional sequence data. Unfortunately, damage to its pleon and sternum obliterated evidence that might have made obvious the presence or absence of a gonopodal plate, leaving that question unresolved. We strongly suspect that the "enclosing sheath" of the gonopod in *G. arenicola*, as reported but only partially illustrated by Thoma *et al.* (2009), could represent yet another variation in this structure, and this species clearly groups with those that have the more obviously developed gonopodal plate. *Glassella miamiensis* and *G. faxoni* share the plate and are closely related both morphologically and genetically (Fig. 1), but we cannot yet determine if *G. leptosynaptae* and *G. vanderhorsti* (at least the latter of which also has the plate) are included in that same well-supported molecular genetic clade for present lack of sequence quality material.

Thorough study of the first pleonal somite in mature males for all other suspected members and close relatives of *Glassella* is required to determine if any homologous ramification of the gonopodal plate may have also in those been thus far overlooked. This is to be undertaken in the course of coming descriptions of the American species "*Pinnixa* sp. (ULLZ 13337 and ULLZ 14141)" from Panama (Fig. 1) and at least three additional new western Atlantic species that clearly represent *Glassella* in morphology, but for which we at present lack sequence quality materials. Further studies must also include molecular and morphological examinations of potentially related species, especially the eastern Pacific American species *Pinnixa bahamondei* Garth, 1957, *P. darwini*, Garth, 1960, *P. hendrickxi* Salgado-Barragán, 2015, *P. pembertoni* Glassell, 1935, and perhaps *P. transversalis* (H. Milne Edwards & Lucas, 1844). From our preliminary morphological observations of materials used in the present molecular study, we can state that a clear ramification of the male gonopodal plate is present in the eastern Pacific species *G. abbotti*, underpinning our inclusion of it in *Glassella* on the basis of more than solely molecular phylogenetics.

Further studies are also required to more thoroughly compare the Indo-West Pacific genus *Indopinnixa* to the American *Glassella*. We retain separation of these genera as sister clades, though only two of the seven species assigned to *Indopinnixa* could for the present be represented in the molecular genetic analysis. Furthermore, only one of these two species was represented by an intact male specimen, the other represented only by a donated tissues sample. The intact male of *I. kumejima* was stained and carefully examined, and no evidence of a gonopodal plate or ramification thereof could be found, suggesting this could be a character of use in separating at least some species of the two genera.

Genus *Rathbunixa* n. gen.

urn:lsid:zoobank.org:act:316B06E6-4F1B-4109-A608-2BAC7E426737

TYPE SPECIES. — *Rathbunixa sayana* (Stimpson, 1960) n. comb. [*Pinnixa*].

DIAGNOSIS. — Carapace broad, regions clearly defined, cardiac ridge sharp, not extending entirely across carapace. Third maxilliped ischiomerus subtrapezoidal; propodus and dactylus longer than carpus, shorter than ischiomerus; dactylus elongate, inserting near base of propodus, reaching beyond end of propodus. Chelipeds hairy or pubescent, no lines of setae or tubercles on palm; fixed finger strongly reduced or deflexed, sexually dimorphic, ontogenetically variable. Ambulatory legs elongate, slender; relative lengths P4 > P3 > P2 > P1. Male pleon tapering toward end, telson subtriangular; lacking gonopodal plate.

ETYMOLOGY. — Named for Mary J. Rathbun, who carefully cataloged, examined and described a large percentage of the pinnotherids presently known to mankind, including this genus. Gender feminine.

ADDITIONAL SPECIES. — *Rathbunixa affinis* (Rathbun, 1918) n. comb. [*Pinnixa*];
Rathbunixa californiensis (Rathbun, 1894) n. comb. [*Pinnixa*];
Rathbunixa occidentalis (Rathbun, 1894) n. comb. [*Pinnixa*];
Rathbunixa pearsei (Wass, 1955) n. comb. [*Pinnixa*].

MATERIAL EXAMINED. — In addition to the material included in the phylogenetic analyses (Table 1) the following samples were available for examination:
Rathbunixa pearsei n. comb. — ULLZ 4421, ULLZ 4425, ULLZ 5513, ULLZ 5590 (8), ULLZ 7024, ULLZ 14001, ULLZ 14006 (2), ULLZ 14007, ULLZ 14010, ULLZ 14082, ULLZ 14085, ULLZ 14515 (3), ULLZ 14910, ULLZ 14913, ULLZ 15032, ULLZ 16744 (2) (Fort Pierce, FL, USA), ULLZ 13947 (Marco Island, FL, USA); MNHN-IU-2017-9366 (= former ULLZ 7026); ULLZ 4496, ULLZ 4498, ULLZ 7401, ULLZ 13542 (4), ULLZ 13547 (2), ULLZ 17455 (2) (Tampa Bay, FL, USA), ULLZ 15749 (Bayport, FL, USA), ULLZ 2594 (5), ULLZ 15671 (Mobile Bay, AL, USA), ULLZ 14041 (Bay St. Louis, MS, USA), ULLZ 14016 (Horn Island, MS, USA), ULLZ 17466, ULLZ 17470 (offshore, northeastern Gulf of Mexico), ULLZ 2593 (Cheniere au Tigre, LA, USA), ULLZ 2596 (Corpus Christi, TX, USA);
Rathbunixa sayana n. comb. — USNM 36323 (Rhode Island, USA), USNM 173396 (North Carolina, USA); MNHN-IU-2017-9367 (= former ULLZ 7397), ULLZ 14906 (2) (Fort Pierce, FL, USA), USNM 48438 (Sarasota Bay, FL, USA).

REMARKS

Morphological similarities among some species of this genus have been noted previously, though always between species sharing an ocean basin such as the eastern Pacific pair, *R. affinis* and *R. occidentalis*, and the western Atlantic pair, *R. pearsei* and *R. sayana* (Rathbun 1918; Wass 1955; Zmarzly 1992). We have observed great variability in the morphological characters that define *R. pearsei* and that are reported to differentiate it from *R. sayana*. Wass (1955) described the former species to separate specimens found in northwestern Florida from *R. sayana*, the distribution of which was known at that time to range from Massachusetts to Sarasota Bay, in southwestern Florida. Later records extended the distribution of *R. sayana* to Grand Isle, Louisiana, and Brazil (Schmitt *et al.* 1973). In addition, we have samples that fit the morphological characters of *R. sayana* from Corpus Christi, Texas. We also have collections of specimens matching the description of *R. pearsei* from Atlantic coast of Florida, Gulf of Mexico waters in southern Florida, and Gulf Shores, Alabama. All these samples are genetically very close in relationship (Fig. 1). This suggests that *R. pearsei* should be regarded as a junior synonym of *R. sayana*. However, the type of *R. sayana* is not extant, and the type locality is the mouth of Beaufort Harbor, North Carolina, a location we were unable to represent among collection sites for our samples of *R. sayana*, all of which are well to the south. Thus, we for now lack genetic evidence upon which to base genetic re-evaluation of these two taxa, and retain both names.

When Rathbun (1894) described *Pinnixa occidentalis* and *P. californiensis* she noted the resemblance between the two, but nonetheless treated them as separate species, though she later synonymized them (Rathbun 1918). However, more recently smaller and less granulate variations of *R. occidentalis* have been reported, indicating that this taxon should be treated as a "group of allied species" (Hart 1982). The specimen we examined is probably one of these variants. Whether or not some of these variants could possibly match the description of *R. californiensis* requires further investigation. For now, we elect to retain *R. californiensis* as a separate taxon, following Ng *et al.* (2008). The material of *R. occidentalis* included here was collected in Panama, expanding the southern limit of the species range, which was formerly Magdalena Bay, in Mexico (Schmitt *et al.* 1973). Despite the fact that we were unable to analyse additional samples of the *R. californiensis* – *occidentalis* complex, we provisionally assign both species to this genus, based on their long recognized relationship.

Genus *Sayixa* n. gen.

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TYPE SPECIES. — *Sayixa monodactyla* (Say, 1818) n. comb. [*Pinnixa*].

ORIGINAL DESCRIPTION FOR *PINNIXA* [*PINNOTHERES*] *MONODACTYLA* (SAY, 1818). — "*P. monodactylum** (male) Thorax transverse; hands monodactyle. […]
Thorax transversely subeliptical, narrowing each side to the middle of the lateral edge, which is rounded, a tubercle each side marking the situation of the anterior lateral angles, surface punctured; *orbits* suborbicular; *anntennæ* [sic], exteriors subequal to the breadth of the clypeus; *hand* oblong, somewhat quadrate; *palm* concave and ciliated in the middle, a spiniform angle instead of a finger, with a tooth at its base, and another at the base of the thumb larger; *thumb* abruptly incurved at base, rectilinear towards the tip, with an angle at the interior middle, tip acute, attaining the tip of the spiniform angle; *feet*, second, fifth and third pairs subequal, the latter rather larger, fourth pair larger, and with the fifth pair with somewhat dilated tibia; *abdomen* with a few larger punctures, terminal joint rounded at tip, entire, ciliated and attaining the tip of the geminate joints of the pedipalpi.
Length three tenths, breadth one half an inch.
This curious animal occurs in the Richmond Museum. Mr. J. Warrell, the proprietor of that interesting establishment, supposes it to be American, but whether from our eastern or western coast he could not say. It is particularity remarkable in having monodactyle hands, a character which in a very rigid arrangement would not only separate it from the genus Pinnotheres, but also from the preceding species as a distinct genus. The tibia of the fourth and fifth pairs of feet are somewhat dilated, but the corresponding tarsi are accidentally wanting in this specimen."

DIAGNOSIS. — Carapace transversally subeliptical, wider than long, punctate, narrowing toward rounded lateral edges; anterolateral margins each with single lobiform tooth or tubercle near or just anterior to lateral extreme. Third maxilliped with ischiomerus subtrapezoidal; propodus and dactylus elongate, longer than carpus; dactylus inserting near base of propodus, reaching beyond end of propodus. Chelipeds heavy, palm lacking longitudinal lines of setae; cheliped fixed finger strongly shortened, reduced to spiniform angle, with sharp tooth at base of dactylus.
First two ambulatory legs (P2, P3) slender, P4 and P5 somewhat stouter; lengths P4 > P3 > P2 > P5. Male pleon subtrapezoidal, somites 4-6 constricted; telson oblong subellipsoidal, much wider than long.

ETYMOLOGY. — Named for Thomas Say, author of the type species of this new genus, and first author to describe pinnotherid species after Linneaus.

MATERIAL EXAMINED. — In addition to the material included in the phylogenetic analyses (Table 1) one sample was available for examination: MNHN-IU-2017-9368 (= former ULLZ 8569) (offshore, northern Gulf of Mexico).

REMARKS

In describing the species *Pinnotheres monodacytlum*, later transferred to *Pinnixa*, Say (1818) indicated that this taxon presented characters that "would not only separate it from the genus *Pinnotheres*, but also from the preceding species as a distinct genus". The "preceding species" he is referring to is *Pinnotheres cylindricum*, which would become later the type of the genus *Pinnixa*. He discusses in that work the differences between the two species and the genus *Pinnotheres*, but he chose to maintain both within the genus *Pinnotheres*. Later, in 1846, Adam White, assistant in the Zoological Deparment of the British Museum, established the genus *Pinnixa* for *P. cylindrica* on the basis of its carapace being much wider than long, its having a larger cheliped palm when compared to *Pinnotheres*, and on the relative lengths of the ambulatory legs. He, however, did not include what we herewith assign to *Sayixa monodactyla* n. comb. in the genus *Pinnixa*, most likely because he had not found the opportunity to examine it. According to Rathbun (1918), *Sayixa monodactyla* n. comb. had not been seen since the type was reported upon. Moreover, the type in Richmond Museum was, also according to her, probably not extant.

Genus *Scleroplax* Rathbun, 1894

Scleroplax Rathbun, 1894: 250.

TYPE SPECIES. — *Scleroplax granulata* Rathbun, 1894, by monotypy when genus was erected.

ORIGINAL DIAGNOSIS BY RATHBUN (1918). — "Carapace transverse, subpentagonal, hard, very convex, regions scarcely indicated, lower or true antero-lateral margin curving gradually into postero-lateral margin, not forming an angle with it as in *Pinnixa.* Ambulatory legs similar, third longest but not unusually long, fourth not noticeably reduced. Ischium of outer maxillipeds rudimentary, merus oblique, palpus three-jointed, the last joint articulating near proximal end of preceding joint. Only a single species known."

DIAGNOSIS OF THE GENUS AS MODIFIED BY CAMPOS (2006). — "Carapace hard, subheptagonal, highly convex dorsally, anterolateral margins not forming angle with posterolateral margins; MXP3 [= third maxilliped] slightly oblique, covers buccal cavity, ischio-merus subtrapezoidal, propodus extending to end of dactylus, both spoon-shaped and larger than carpus. WL1-4 [= walking leg] of similar shape, third pair slightly longer, fourth not noticeably reduced."

DIAGNOSIS. — (Modified from Rathbun 1918 and Campos 2006). Carapace transverse, subpentagonal or oblong, hard, very convex, anterolateral margins not forming an acute angle with posterolateral margins; cardiac ridge, if present, not extending entirely across carapace. Third maxilliped slightly oblique, covering buccal cavity, ischiomerus subtrapezoidal; propodus and dactylus elongate, longer than carpus; dactylus inserting near base of propodus, reaching end of propodus or slightly beyond. Male cheliped strong, fixed finger somewhat shortened, straight; female cheliped feeble, fixed finger straight; external palm surface sometimes with longitudinal line of tubercles. Walking pereopods subequal, cylindrical, relative lengths P4 > P3 ≥ P2 > P5. Male pleon tapering toward end, telson subsemicircular; first pleonal somite lacking gonopodal plate between gonopods.

ADDITIONAL SPECIES. — *Scleroplax faba* (Dana, 1851) n. comb. [*Pinnixa*];
Scleroplax franciscana (Rathbun, 1918) n. comb. [*Pinnixa*];
Scleroplax littoralis (Holmes, 1894) n. comb. [*Pinnixa*];
Scleroplax schmitti (Rathbun, 1918) n. comb. [*Pinnixa*];
Scleroplax tubicola (Holmes, 1894) n. comb. [*Pinnixa*].

MATERIAL EXAMINED. — In addition to the material included in the phylogenetic analyses (Table 1) the following samples were available for examination:
Scleroplax franciscana n. comb. — ULLZ 5625, ULLZ 5626 (Bodega Bay, CA, USA);
Scleroplax littoralis n. comb. — ULLZ 8505 (10) (Poulsbo, WA, USA), ULLZ 14072 (4) (Gamble Bay, WA, USA);
Scleroplax schmitti n. comb. — ULLZ 14036, ULLZ 14842 (8) (Baranof Island, AK, USA), ULLZ 14117, MNHN-IU-2017-9369 = former ULLZ 14119 (Japonski Island, AK, USA);
Scleroplax tubicola n. comb. — ULLZ 14116 (Middle Island, AK, USA), ULLZ 14118 (Japonski Island, AK, USA).

REMARKS

Genetic distances and the morphological differences observed among some of the species in this group are similar to those shown among conspecific populations in other pinnotherid genera, for instance *Austinixa*, *Tumidotheres* Campos, 1989, or *Tunicotheres* Campos, 1996. Furthermore, for some species there seems to be striking variation in key characters between juveniles and adults. For example, juveniles of *P. littoralis* and *P. faba* appear to be extremely difficult to discriminate (Zmarzly 1992). A more detailed investigation with larger sample sizes and markers appropriate to determine variability between populations of these species is required to clarify phylogenetic relationships within and among them. In addition, knowledge of host associations is required to accompany samples, as these taxa might represent species complexes of separate, but morphologically similar, populations that have adapted to different hosts, which may also be reflected in variations between inshore and offshore samples.

The only specimen of *Pinnixa scamit* available for molecular analyses and morphological examination was a juvenile (UF 11969), and had therefore been identified provisionally. Genetically it was closely allied to *Scleroplax*, however, morphologically it showed characters similar to those in *Rathbunixa* n. gen. It had long slender legs, somewhat compressed, and a sculpted carapace. Despite the results of the molecular analysis, we choose not to transfer *Pinnixa scamit* to the genus *Scleroplax*, until specimens definitively identifiable as *P. scamit* are available for analysis.

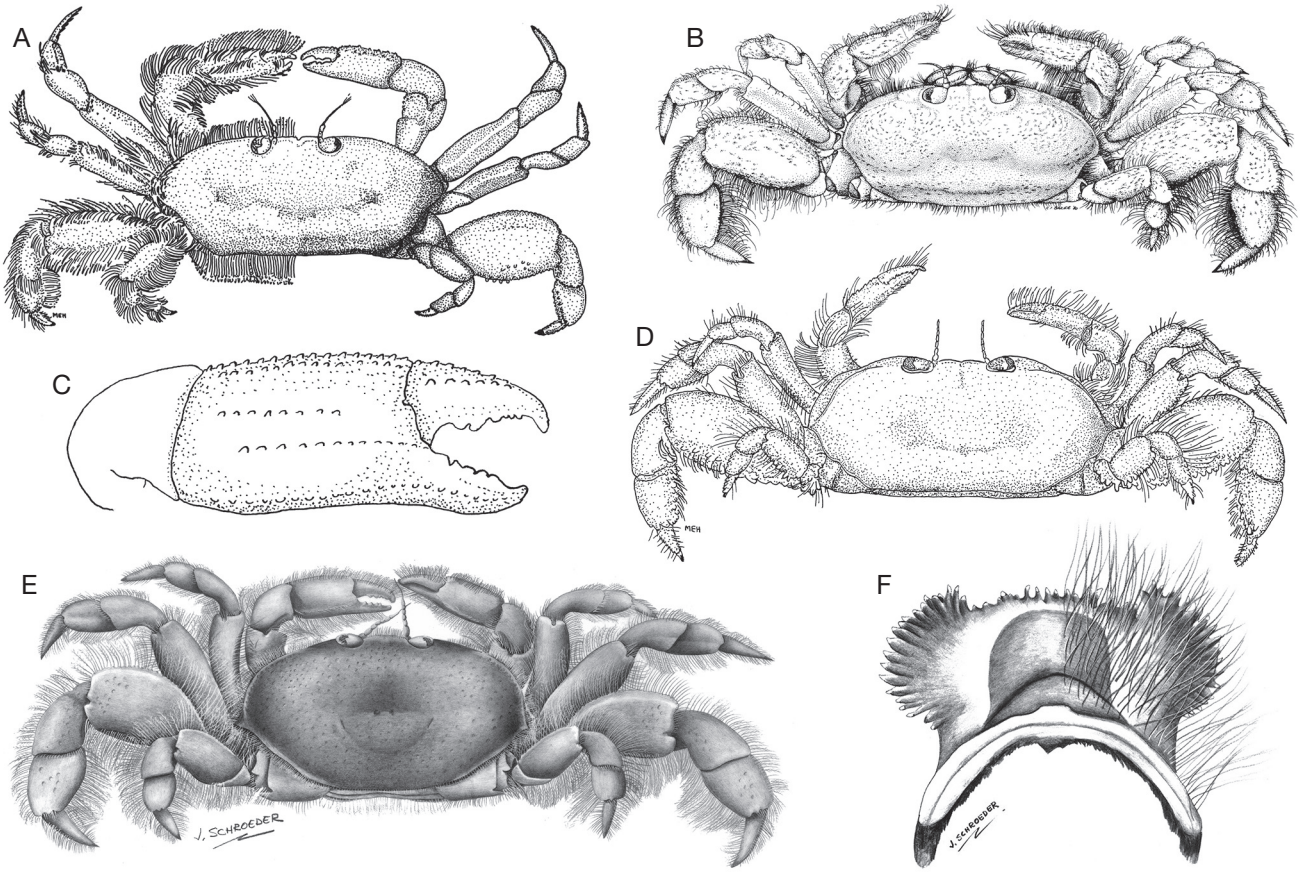

FIG. 5. — Illustrations of selected type and topotypic materials for *Glassella* spp., by Smithsonian artists MEH, Charisse Baker, and Jack Schroeder, predating loss of subject specimens: **A**, *G. faxoni* (Rathbun, 1918) n. comb., habitus, male paratype, cw 10.1 mm, USNM lot 7639; **B**, *G. faxoni* n. comb., left chela external surface, male holotype, cw 11.0 mm, USNM lot 7639; **C**, *G. miamiensis* (McDermott, 2014) n. comb., habitus, male, cw 4.7 mm, HBOI uncatalogued specimen from Indian River, Florida; **D**, *G. floridana* (Rathtbun, 1918) n. comb., habitus, male holotype, cw 6.7 mm, USNM 6996; **E**, *G. vanderhorsti* (Rathbun, 1922) n. comb., habitus, male holotype, cw 6.0 mm, Zoological Museum Amsterdam, now Netherlands Naturalis Biodiversity Center; **F**, *G. vanderhorsti* n. comb., gonopodal plate pleonal surface, male holotype, cw 6.0 mm, Amsterdam Museum.

Genus *Tubicolixa* n. gen.

urn:lsid:zoobank.org:act:00ADBC20-FD16-4594-B5FB-A7DE037E3E8F

TYPE SPECIES. — *Tubicolixa chaetopterana* (Stimpson, 1860) n. comb. [*Pinnixa*].

DIAGNOSIS. — Carapace uneven, regions clearly limited by depressions, some surfaces heavily pubescent, especially margins; cardiac region with transverse crest, not extending entirely across carapace; branchial regions with granulate or serrated edges. Third maxilliped with ischiomerus subtrapezoidal; propodus and dactylus longer than carpus, shorter than ischiomerus, elongate; dactylus inserting near base of propodus, reaching beyond end of propodus. Chelipeds strongly developed, setose, with shortened or deflexed fixed finger, in some cases sexual dimorphism. First two ambulatory legs (P2 and P3) slender, third and fourth (P4 and P5) stouter; relative lengths P4 > P3 > P2 > P5. Male pleon tapering toward end, telson subsemicircular; first pleonal somite lacking gonopodal plate between gonopods.

ETYMOLOGY. — Named *Tubicolixa* in recognition of the group apparent preference for polychaete tubes as a habitat. Gender feminine.

ADDITIONAL SPECIES. — *Tubicolixa brevipollex* (Rathbun, 1898) n. comb. [*Pinnixa*];
Tubicolixa rapax (Bouvier, 1917) n. comb. [*Pinnixa*].

MATERIAL EXAMINED. — In addition to the material included in the phylogenetic analyses (Table 1) the following material was available for examination:
Tubicolixa chaetopterana n. comb. — ULLZ 12480 (Beaufort, NC, USA), ULLZ 4452 (2), ULLZ 4561 (2), ULLZ 5553 (2), ULLZ 6429, ULLZ 7395, ULLZ 7400, ULLZ 10286, ULLZ 14005 (2), ULLZ 14008 (6), ULLZ 14110, ULLZ 14907 (4), ULLZ 14911, ULLZ 17925 (Fort Pierce, FL, USA), ULLZ 14916 (Peanut Is, FL, USA), ULLZ 5542 (7) (Florida Keys, USA), MNHN-IU-2017-9370, ULLZ 17456 (2) (Tampa Bay, FL, USA), ULLZ 14080 (2) (St. Mark's lighthouse, FL, USA), ULLZ 14996, ULLZ 14997 (2) (St. Joseph's State Park, FL, USA), ULLZ 8638 (2), ULLZ 14875 (3) (St. Andrew's Bay, FL, USA), ULLZ 14024 (2) (Perdido Key Beach, FL, USA), ULLZ 8657 (7) (offshore Mississippi, USA), ULLZ 5552 (2) (Isles Dernieres, LA, USA), ULLZ 14832 (Bryan Mound, TX), ULLZ 2597 (3) (Padre Island, TX, USA).
Tubicolixa rapax n. comb. — ULLZ 14115 (Ubatuba, Brazil).

REMARKS

Genetic and morphological differences between specimens of *T. chaetopterana* (Stimpson, 1860) n. comb. from Venezuela and

PROVISIONAL MORPHOLOGICAL KEY TO AMERICAN GENERA OF PINNIXINAE ŠTEVČIĆ, 2005

The present key must be regarded as provisional since many couplets require mature males, and these are not known or available for all species of each genus. Thus, it cannot be ruled out that exceptions to some of the applied characters may occur. It also includes one generic level taxon that remains to be named.

1. Carapace cardiac region posterior surface crossed from side to side by single sharp continuous ridge (most commonly associated with burrowing callianassid ghost shrimps, western Atlantic and eastern Pacific) (see Manning and Felder, 1989 for quality illustrations and examples) ..... *Austinixa* Heard & Manning, 1997
— Carapace cardiac ridge, if present, not crossing the surface of carapace completely (most commonly associated with burrowing worms, mollusks, and upogebiid mud shrimps) 2

2. Maxilliped 3 dactylus large and heavy, as long as or longer than propodus, oriented in a wide angle, sometimes near perpendicular relative to it (Fig. 2H), or (for *Glassella costaricana*) dactylus strongly reduced, inserted subdistally (Fig. 2G); carapace ovate, punctate, regions usually poorly marked; external surface of chela palm often bearing longitudinal ridges or lines of granules, sometimes setose (Fig. 2E); male pleon often with fused segments, telson broader than preceding segment (Fig. 2I) 3
— Maxilliped 3 dactylus reaching to or slightly beyond the end of the propodus, dactylus and propodus elongated, oriented parallel or nearly parallel to each other (Fig. 2C, L, P, T, X); carapace varies; male pleon without fused segments, telson shape varied 5

3. Male pleon with telson short, broader than long, semiellipsoid (Fig. 2I); carapace punctate (western Atlantic, eastern Pacific) ..... *Glassella* Campos & Wicksten, 1997
— Male pleon with telson semicircular, inflated, nearly as long as broad; carapace smooth, forming angle at lateral edges ..... ("*Pinnixa* sp." ULLZ 13337, ULLZ 14141)

4. Mature cheliped fingers not strongly deflected from longitudinal axis of propodus, fixed finger not deflected ventrally from longitudinal axis (Fig. 2B, S); carapace convex, regions poorly marked (Fig. 2A, R) 5
— Mature cheliped fixed finger deflected ventrally from longitudinal axis of propodus, often shortened (Fig. 2K, O, W); carapace varied 6

5. Cheliped fixed finger not conspicuously shortened relative to palm, chelae with little sexual dimorphism, ridge on fixed finger continuing partially on palm (Fig. 2B); carapace lateral angles setose (Fig. 2A); male pleon with telson semiellipsoid (Fig. 2D) (western Atlantic) ..... *Pinnixa* White, 1846
— Cheliped fixed finger somewhat shortened relative to palm, male cheliped strong, female cheliped feeble, in some cases line of tubercles on chela palm, but no conspicuous ridge (Fig. 2S); carapace lateral angles rounded, with no patches of setae (Fig. 2R); male pleon with telson semicircular (Fig. 2U) (northeastern Pacific coasts, Alaska to Mexico) ..... *Scleroplax* Rathbun, 1983

6. Male pleon with telson elongate, more than twice as wide as long (Fig. 2Q); mature cheliped fixed finger strongly reduced, replaced by a spiniform angle of propodus, sharp tooth at the base of dactylus (Fig. 2O); carapace anterolateral margins without tuberculate ridge, each with single lobiform tubercle just anterior to lateral extreme (Fig. 2N) (western Atlantic) ..... *Sayixa* n. gen.
— Male pleon with telson semicircular or semitriangular, not more than twice as wide as long (Fig. 2M, Y); mature cheliped fixed finger varied, if spiniform, with no additional sharp large tooth at the base of dactylus (Fig. 2K, W); carapace anterolateral margins often with tuberculate ridge, no conspicuous tubercle near lateral extreme (Fig. 2J, V) 7

7. Ambulatory legs (P2–P4) subequal, slender, compressed, dactyli long and slender, nearly as long as propodi; carapace regions clearly defined, branchial region crossed by tuberculate ridge (Fig. 2J); male pleon with telson subtriangular (Fig. 2M) (western Atlantic, eastern Pacific) ..... *Rathbunixa* n. gen.
— First ambulatory legs (P2 and P3) slender, next two pairs (P4 and P5) swollen, dactyli strong, shorter than propodi; carapace regions clearly defined, branchial region with no conspicuous tuberculate ridge (Fig. 2V); male pleon with telson semicircular (Fig. 2Y) (western Atlantic) ..... *Tubicolixa* n. gen.

Belize and those from the Gulf of Mexico and North Atlantic coasts at minimum suggest population structure within this species. This taxon may represent a species complex, similar to that observed for some of the species of *Scleroplax*, with different morphotypes at the species and/or population level likely adapted to different habitats and/or hosts. However, most preserved samples available to us at present do not represent sequence quality materials. Additional studies with larger and more broadly representative sample sizes based on markers with resolution at the population level should be undertaken, along with more detailed collection information regarding habitat and hosts. Additional samples of *T. chaetopterana* n. comb. from Belize should further clarify the identification of that juvenile specimen, once at least a 12S sequence for can be obtained.

The holotypes of *Pinnixa brevipollex* Rathbun, 1898 (USNM 21593, near La Plata estuary, Argentina) and *Pinnixa rapax* Bouvier, 1917 (MCZ 10997, Gulf of San Matías, Argentina) require further study and comparison, along with molecular and morphological studies based on contemporary samples representing their putatively separate populations. These species have been suggested to be synonyms, but the holotypes remain to be compared (Fenucci 1975; Bezerra *et al.* 2006). Some authors suggest there are differences in the male pleon (Righi 1967), but the allegedly junior synonym *P. rapax* is still considered a valid species (Ng *et al.* 2008). This group may represent yet another species complex, and we elect to for now continue their treatment as separate taxa.

DISCUSSION

Polyphyly of *Pinnixa*

The results indicated *Pinnixa s.l.* to be a highly polyphyletic genus, supporting inferences of previous studies based on molecular evidence as well as adult and larval morphology (Cuesta *et al.* 2002; Palacios Theil *et al.* 2009, 2016). The present analyses, being limited to sequence-quality specimens, could represent only 17 of 51 currently recognized extant species that are assigned to *Pinnixa s.l.*, but our analyses did include the type of the genus, *P. cylindrica*. While 13 additional species in five genera presently within the subfamily Pinnixinae, as well as members of the family Pinnixulalinae, were available for inclusion, only two species belonging to the Indo-Pacific genus *Indopinnixa* could be studied. None of the seven species that are presently included within the genus *Pinnixa* and inhabit Indo-Pacific waters, including the Red Sea and the Persian Gulf, could be analyzed.

Interoceanic phylogenetic associations among pinnotherid taxa in the subfamily Pinnotherinae have been observed in some cases, for example between species of the American genus *Zaops* Rathbun, 1900 and European species in *Nepinnotheres* Manning, 1993, or between the European *Pinnotheres* and Asian species of *Alain* Manning, 1998 (Palacios Theil *et al.* 2016). Similar relationships could be found here for *Indopinnixa* and others might become evident once these species are included in molecular and further morphological studies. In addition, specimens of *Alarconia* Glassell, 1938 must be analyzed. For *Alarconia* only two species are known, one from Pacific coasts of Mexico and another from Brazil, and their relationships remain in question. The seven described species placed in *Indopinnixa* are restricted to Indonesia, Hong Kong, and Japan. Nevertheless, the genetic evidence presented here shows their close relationship to the *Pinnixa faxoni* complex. This is in accordance with morphological similarities among these species that have been previously suggested by Naruse & Maenosono (2012).

No representatives of the subfamily Pinnixinae included in our molecular analyses were genetically closely allied to *P. cylindrica*, the type species of the genus. While sharing a carapace wider than long and the third ambulatory leg (P4) longer than the others, none of these subfamilial representatives grouped in the same molecular genetic clade with the type. Instead, they were separated at greater genetic distances, typically consistent with differences between genera. Among presently known members of Pinnixinae, including those unavailable for the present molecular phylogenetic analyses, none are known to be more similar morphologically to *P. cylindrica* than are *P. lunzi* Glassell, 1937 and *P. monodactyla*. However, no sequence quality material for *P. lunzi* was available to us and *P. monodactyla* did not in our analyses show grouping at the level of genus with *P. cylindrica* or with any of the species available and presently placed in *Pinnixa s.l.* Like the other taxa, *P. monodactyla* has a carapace that is wider than long and third ambulatory legs that are longer than the others. In addition, its third maxilliped is similar to those in *P. cylindrica* and those of *Austinixa*, *Scleroplax*, and the *P. sayana*, and the *P. chaeopterana* complexes. However, the morphology of the cheliped, shape and ornamentation of the carapace, and especially the male pleon in *P. monodactyla* differ from those of the aforementioned species. In *P. monodactyla* the fixed finger or thumb of the cheliped is more strongly reduced than in any of the other species, and has been replaced by a spiniform angle of the palm. Also, unlike for the other species that share its maxilliped form, *P. monodactyla* has a male pleonal telson that is wider than the subterminal pleonal segment.

Taxonomic implications

While full understanding of group relationships must await access to additional sequence-quality specimens for a robust representation of morphological variants, present results indicate that eighteen species of *Pinnixa* as well as the three species in *Laminapinnixa*, *L. faxoni*, *L. miamiensis*, and *L. vanderhorsti*, warrant reassignment. Some species can be assigned to *Scleroplax* and others to *Glassella*, but three new genera are justified to accommodate those species most closely related to *P. chaetopterana*, those allied to *P. sayana*, and a third genus to receive *P. monodactyla*, as treated in the present paper.

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