

Molecular and morphometric systematics of *Diapterus* (Perciformes, Gerreidae)

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The fish belonging to Gerreidae are common representatives of the coastal ichthyofauna of the tropics and subtropics of the world. The genus *Diapterus* has a neotropical distribution and currently includes four species: two in the Atlantic Ocean [Irish mojarra *D. auratus* Ranzani 1842 and rhombic mojarra *D. rhombeus* (Cuvier 1829)] and two in the Pacific Ocean [short-beaked mojarra *D. brevirostris* (Sauvage 1879) and golden mojarra *D. aureolus* (Jordan & Gilbert 1882)]. This genus has uncertain taxonomy based on the remarkable and dissimilar morphology of *D. aureolus*. We evaluated the taxonomy and phylogeny of *Diapterus* with statistical (canonical discriminant analysis) and phylogenetic analyses (maximum parsimony, maximum likelihood and Bayesian inference) of geometric morphometric data (relative warps) and molecular data (12Sr RNA, 16Sr RNA, COI and RAG1 sequences). Our results indicate that the genus *Diapterus* as we currently conceive it is a polyphyletic group: [(*Gerres cinereus* – *Eucinostomus* spp. (*D. aureolus* – (*Eugerres* spp. (*D. auratus* – (*D. brevirostris* – *D. rhombeus*)))))]. Therefore, a taxonomic rearrangement is needed. To preserve the monophyly of the group, our proposal is to remove *D. aureolus* and place it in a new monotypic genus. A neotype is designated for *D. aureolus* as well as an artificial identification key for the genera and the species treated in this article.

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Our concept of a species is necessarily shaped by our understanding of the characters by which it attains objective and testable status in taxonomic research, [however] there is a disturbing trend to ignore deep thought about individual characters and to treat species

as if they existed to be recognized by DNA barcodes rather than critically tested as evolutionary hypotheses. Those who misuse taxonomic information can answer for their own sins.

(Valdecasas *et al.* 2013)

Introduction

The fish of the genus *Diapterus* belong to the Gerreidae family, commonly known as mojarras or silver biddies. This family has a circumglobal distribution within the tropics and subtropics, preferentially inhabiting areas with sandy and muddy bottoms (Deckert & Greenfield 1987; Castro-Aguirre *et al.* 1999). Distribution and abundance of these fish and its ecological and fisheries' importance have been the subject of countless studies over the last 150 years (e.g. Austin 1971; Arenas-Granados & Acero 1992; Rivas *et al.* 1999; Costa *et al.* 2010).

However, taxonomy of Gerreidae has been confusing and an active issue of discussion among ichthyologists (e.g. Chen *et al.* 2007; De La Cruz-Agüero *et al.* 2012). Currently, eight genera are recognized, but taxonomic status of more than 50 nominal species has not yet been revised, and some gerreid taxa in the Neotropics are still treated by some authors as species *inquirendae* (e.g. validity and/or generic assignment uncertain or questionable). This includes *Ulaema lefroyi*, *Eucinostomus havana*, *Eugerres periche*, *Eugerres brevimanus* and *Gerres simillimus*.

The genus *Diapterus* was described by Ranzani in 1842 and re-diagnosed by Jordan and Evermann (1927). It is composed by four species found on both coasts of America. The Irish mojarrá *D. auratus* Ranzani 1842 and the rhombic mojarrá *D. rhombeus* (Cuvier 1829) are located in the Atlantic Ocean (Castro-Aguirre *et al.* 1999), while the short-beaked mojarrá *D. brevirostris* (Sauvage 1879) and the golden mojarrá *D. aureolus* (Jordan & Gilbert 1882) are distributed in the Pacific Ocean (Allen & Robertson 1994). *Diapterus* species can be distinguished from other Neotropical gerreids by the serrated inferior margins of the preoperculum, absence of serrations on the preorbital bone, body coloration, pharyngeal arch morphology and thickness of dorsal and anal fin spines (Bussing 1995).

Diapterus, like many other Gerreidae, has taxonomic and nomenclatural problems, initially considered as *Gerres* (see Jordan & Gilbert 1882), which also included all species currently recognized in genus *Eugerres* (e.g. Evermann & Meek 1883, 1886; Andreato 1988; Miller 2005) and once synonymized with *Moharra* (e.g. Poey 1875; Meek & Hildebrand 1925). A nomenclatural problem was recently solved, establishing the validity of *D. brevirostris* over *D. peruvianus* (González-Acosta *et al.* 2007). Current concerns are about the number of valid species from a group of eight nominal species (Deckert & Greenfield 1987; González-Acosta *et al.* 2007).

One problem that remains unsettled within the genus, 40 years after Deckert (1973) first noticed it, is the taxonomy and phylogenetic relationships of *D. aureolus*. This taxon was proposed as a new genus in his unpublished

master's thesis because it was unique among species in *Diapterus* and *Eugerres* by possessing separate dorsal fins, a high gently curved lateral line and an oval lateral body outline (Deckert 1973). Álvarez-Pliego (2010) using osteological characters ranked *D. aureolus* as a subgenus within *Diapterus*. Recently, Vergara-Solana *et al.* (2013) showed that growth patterns and shape variation of *D. aureolus* are the most distinct within this genus. Despite the degree of morphological dissimilarity, *D. aureolus* was retained within the genus.

The morphological uniqueness of *D. aureolus* has not been evaluated in a phylogenetic context. Under this approach, the taxonomic assessment of any group should be based on a phylogenetic hypothesis, preferably using molecular techniques, such DNA sequence analysis and morphological data (De Ley 2000). Our goal was to explore the the relationships of *Diapterus* spp., proposing for the first time a phylogenetic hypothesis based both on morphological (geometric morphometric) and molecular data.

Molecular phylogenies of selected neotropical Gerreidae species indicate the existence of two distinct clades: *Diapterus* + *Eugerres* and *Eucinostomus* + *Gerres*; however, no specimens of *D. aureolus* were included (Espinosa *et al.* 1993; Ruiz-Carus & Uribe-Alcocer 2003a,b; Chen *et al.* 2007). These phylogenetic clades agree with the morphological assemblages characterized by the shape of preoperculum and preorbital bone (Bussing 1995), and in one otolith shape analysis by De La Cruz-Agüero *et al.* (2012).

The application of geometric morphometric analysis to evaluate phylogenetic relationships in Gerreidae, to our knowledge, has not been previously attempted. This study combines morphometric and molecular characters for a phylogenetic analysis of *D. aureolus* and related species, to infer its taxonomic position within Gerreidae.

Materials and methods

Taxon sampling

Specimens and tissue samples used for the geometric morphometric and molecular analyses partly belong to the Colección Ictiológica del CICIMAR-IPN (CI) in La Paz, B.C.S., Mexico. Additional revised materials came from different scientific collections (see Material examined section): Ciencias de Mar y Limnología, Mazatlán (EMU-P) of the Universidad Nacional Autónoma de México (U.N.A.M.); Instituto de Biología (IBUNAM-P); Universidad de Costa Rica (UCR); Florida State Museum, University of Florida (UF-FSU); American Museum of Natural History (AMNH); and the California Academy of Sciences, Department of Ichthyology (CAS, including holdings of the Stanford University, SU). Tissue samples came from

specimens captured between 2008 and 2010, mostly from local fishermen, and occasionally by the authors collecting specimens during field work. Collection of specimens was under the permit granted to the CI (Fig. 1).

All examined specimens are currently held in the CI and are available on request (see details on the CI website: <http://coleccion.cicimar.ipn.mx>). The sex was not considered separately because gerreid fish do not have sexual dimorphism (De La Cruz-Agüero & Galvan-Magana 1993).

Morphometric data

Among all sampled fish ($n = 171$), *D. auratus* ($n = 20$), *D. aureolus* ($n = 72$), *D. brevirostris* ($n = 38$) and *D. rhombus* ($n = 40$) body size ranged from 52.9 mm standard length (SL) in *D. aureolus* to 216.7 mm SL in *D. auratus*. For this range of size, allometric bias is negligible (Vergara-Solana *et al.* 2013). Given that the samples came from different locations across the range of the four species, we believe this study reflects a large part of the variability within and between the species.

The left side of each fish was photographed with a digital camera (Olympus® SP 320, Shinjuku, Tokio, Japón) with $3\times$ optical zoom and a light source (Olympus® SZ2-LGBST) mounted on a base that includes a metric scale. Twelve landmarks and four semi-landmarks (see Fig. 2 A) were recorded to best represent the fish body shape, using the TPSDIG 1.4 program (Rohlf 2004). Coordinates were superimposed by the procedure of Generalized Procrustes Analysis (GPA) (Rohlf & Slice 1990) in CoordGen6 (<http://www2.canisius.edu/~sheets/morphsoft.html>) devel-

oped by Sheets (2004). Additionally, semi-landmarks were aligned using SemiLand (Sheets 2004). The superimposed and aligned configurations were then projected onto an orthonormal space that is tangent to Kendall's shape space. Differences in shape are described as deviations from the mean configuration (Bookstein 1989; Rohlf 1993). Partial warp scores (PWs), including both uniform and non-uniform components, were used as descriptors of shape variation (Bookstein 1991; Rohlf 1993; Rohlf *et al.* 1996).

Molecular data

Total DNA was extracted from muscle samples from each species of *Diapterus*, using a Qiagen extraction kit (catalog no. Q01-69506, Hilden, Germany). Three mitochondrial gene fragments (12SrRNA, 16SrRNA and COI) and a fragment of a nuclear gene (RAG1) were amplified. Amplifications were performed using the primers L1091 and H1478 for the 12SrRNA (Kocher *et al.* 1989); 16Sar-L and 16Sbr-H for the 16SrRNA (Palumbi 1996); and FishF1 and FishR1 for the COI (Ward *et al.* 2005). We used two pairs of primers to obtain a relatively long sequence of about 1400 pb for RAG1. We designed these primers based on one sequence of *Diapterus auratus* deposited in GenBank (Accession Number EF095664.1). DauraRAG1F1 (ATCTCTGGATGGGCTTCCTC) and DauraRAG1R1 (AAAAGGGGTTGGTTCTCCAT) were used in one reaction; and DauraRAG1F2 (GATGAGAAGATGGTGC GTGA) and DauraRAG1R2 (CCAGGGTCTTGTG-CAGGTAA) were used in the other reaction. The fragments obtained independently from both reactions were combined for posterior analyses.

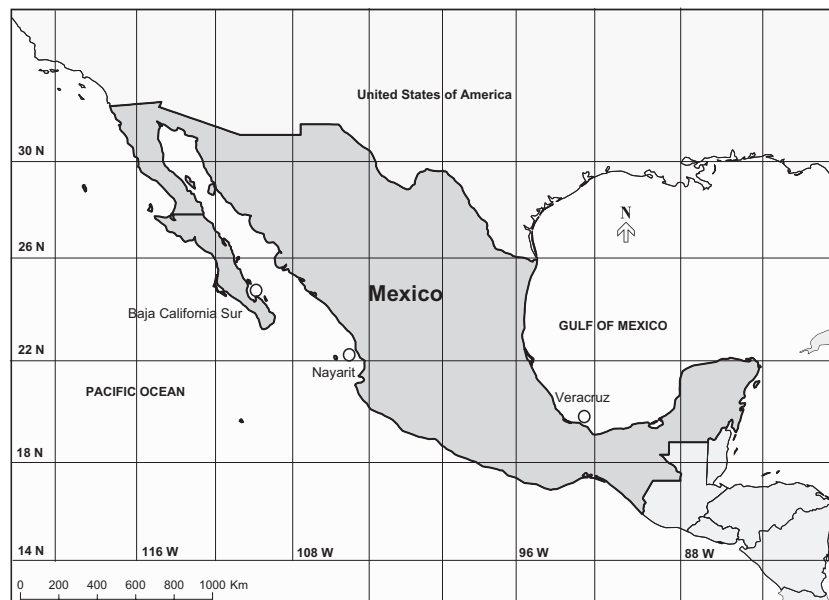


Fig. 1 Locations where tissue samples were obtained for molecular analysis (hollow circles).

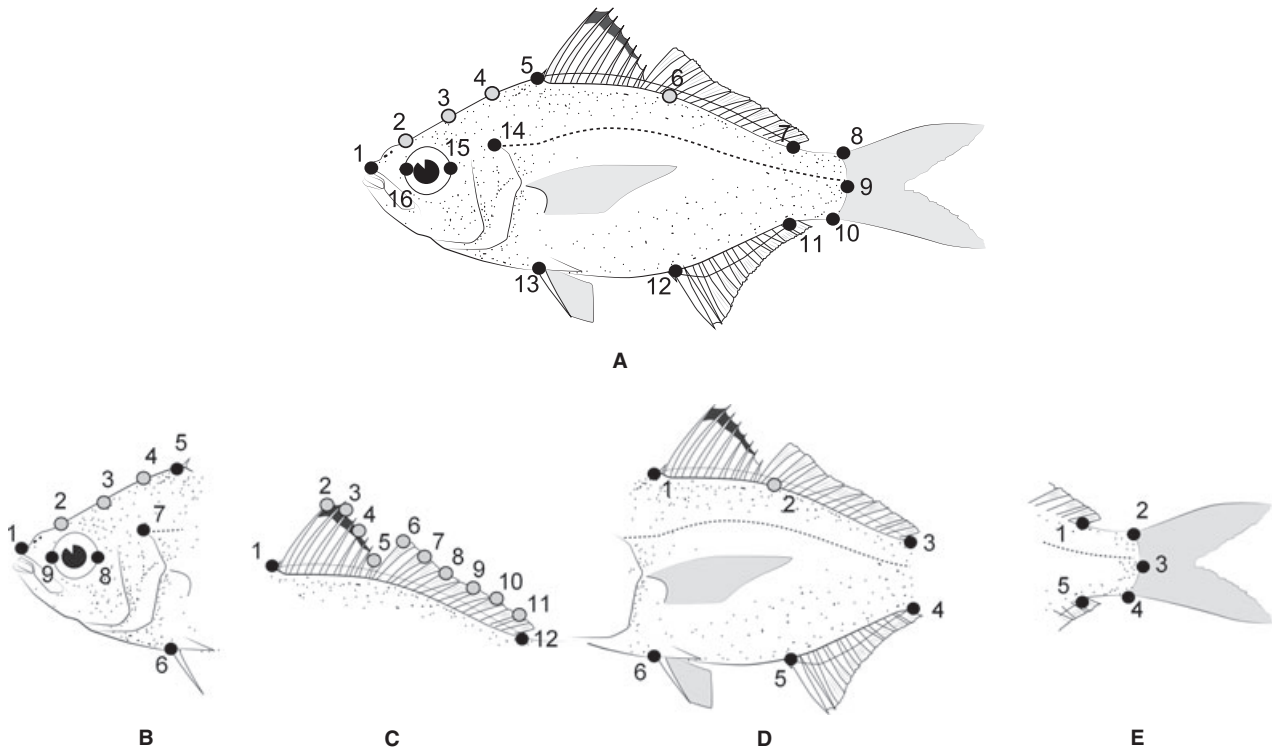


Fig. 2 Graphic representation of the mark configuration used to represent shape for morphometric analysis (A) and those used to generate the relative warps (RWs) for the phylogenetic inference (B–E). —A. Grey dots represent semi-landmarks, and black dots represent landmarks: 1 = tip of the snout, 5 = anterior insertion of the dorsal fin, 7 = posterior insertion of the dorsal fin, 8 = dorsal insertion of the caudal fin, 9 = intersection of lateral line and the caudal fin, 10 = ventral insertion of the caudal fin, 11 = posterior insertion of the anal fin, 12 = anterior insertion of the anal fin, 13 = anterior insertion of the pelvic fin, 14 = dorsal end of the operculum, 15 = posterior margin of the eye, 16 = anterior margin of the eye. —B. Cephalic region, —C. dorsal fin, —D. thoracic region, —E. caudal peduncle.

Each reaction was performed using a 35 μ L volume containing: 1 \times PCR buffer (Invitrogen, Carlsbad, CA, USA), 0.2 μ M dNTP mix, 0.48 μ M of each primer, 4.0 mM MgCl₂ and 2.5 U Taq DNA polymerase (Invitrogen). Thermal cyclers conditions for amplification consisted of an initial phase of 2 min at 94 °C, followed by 35 cycles, and a final extension for 4 min at 72 °C. Each of the 35 cycles consisted of three steps: (i) 1 min at 94 °C; (ii) 1 min at 58 °C for 12 and 16 s; 1 min at 66.5 °C for the RAG1, and 30 s at 54 °C for the COI; (iii) 2 min at 72 °C.

Available GenBank sequences of related species that were used as outgroups are the Jenny mojarra, *Eucinostomus gula* (Quoy & Gaimard, 1824), EF095598.1 (12Sr RNA); EF095570.1 (16Sr RNA), EF095663.1 (COI) and GU225236.1 (RAG1); the striped mojarra, *Eugerres plumieri* (Cuvier 1830), EF095600.1 (12Sr RNA); EF095572.1 (16Sr RNA); EF095665.1 (COI), and GU225258.1 (RAG1); and the yellow fin mojarra, *Gerres cinereus* (Walbaum, 1792), EF095601.1 (12Sr RNA); EF095573.1 (16Sr RNA); EF095666.1 (COI), and GU225291 (RAG1). All sequences generated in this study were deposited in the GenBank (Accession Numbers: KJ468671 - KJ468686).

Geometric morphometric analysis

Comparison of shapes among the four species of *Diapterus*, as *a priori* groups, was performed by canonical discriminant analysis (CDA) of the partial warps scores (PWS) using the CVAGen6 program (<http://www2.canisius.edu/~sheets/morphsoft.html>) developed by Sheets (2004). Our question was whether there is a difference between the mean shapes of species. The tests of significance of the canonical variate axes are based on the Wilk's Lamda value.

Classification efficiency, such as the estimated error rates in CDA, was cross-validated according to procedures described by Lachenbruch and Mickey (1968). The bias of the classification was determined with the Cohen-Kappa (κ) coefficient, which estimates the improvement over chance of corrected classification rates (Tuset *et al.* 2003). Values of κ range from 0 to 1, with zero indicating that discriminant analysis yielded no improvement over chance and 1 indicating perfect agreement (Titus *et al.* 1984). The κ values were scaled up to a percentage, and the prior probability of classification was equal for all groups. Finally, a G-test of independence was used to test agreement between observed classification rates and expected

classification rates (Tuset *et al.* 2003). The superimposition process and CDA were completed in CVAGen6 (Sheets 2004).

Phylogenetic reconstructions

Morphometric phylogeny. For phylogenetic reconstructions, the dark-spot mojarra *Eucinostomus entomelas* Zahuranec in Yáñez-Arancibia 1980, the streaked mojarra *Eugerres lineatus* (Humboldt 1821) and the yellow fin mojarra *Gerres cinereus* (Walbaum 1792) were used as outgroups.

Morphometric data of body shape were divided into three structural regions: head, thorax and caudal peduncle. Landmarks of the dorsal fin were included in the analysis (Fig. 2B–E). Superimposition of each structure was performed by GPA (Rohlf & Slice 1990; Rohlf 1999), employing COORDGEN6 program (Sheets 2004).

The relative warp scores (RWs) were obtained separately for each structure, using the principal component analysis PCAGen6 program (<http://www2.canisius.edu/~sheets/morphsoft.html>) developed by Sheets (2004). A PCA was applied separately for each data set. The RWs were averaged for each species and pooled (Rohlf 2002). Phylogenetic analysis was executed using the average of the RWs for each species. Previously, RWs have proved useful for describing phylogenetic relationships (e.g. Rohlf *et al.* 1996; Monteiro 2000; MacLeod 2002; Acero *et al.* 2005). Phylogenetic analyses of morphometric data (e.g. RWs) were performed using maximum parsimony (MP) and maximum likelihood (ML) for continuous characters. Phylogenetic trees under MP were generated with the implicit enumeration search criterion, as implemented in TNT 1.1 (Goloboff *et al.* 2008). The ML trees were estimated by the CONTML module of PHYLIP 3.2 (Felsenstein 1973). The jackknife monophyly index (JMI) was calculated to assess the relative stability of the clades (Siddall 1995).

Molecular phylogeny. We used the TNT 1.1 program (Goloboff *et al.* 2008) to generate the ML trees, using implicit enumeration. The JMI was used as a measure of clade support (Siddall 1995). The best substitution models were chosen for each gene, according to the Bayesian information criterion (BIC) and AIKAIKE criteria (AIC) obtained in the program jMODELTEST (Posada 2008). A Bayesian framework (BI) was also evaluated using the program Mr. BAYES 3.1.2 (Huelsenbeck & Ronquist 2001). The tree search consisted of two independent runs of 2 000 000 generations sampled every 1000. The program TRACER 1.5 (Rambaut & Drummond 2007) was used to explore mixing of parameters and convergence of the runs. After reaching convergence, the first one-fourth of the samples (parameters and trees) was removed.

Results

Geometric morphometric analysis

The canonical discriminating analysis (CDA) recovered three canonical variates, which revealed significant differences between four species (CV1 $\lambda = 0.0108$, $\chi^2 = 697.9$, d.f. = 84, $P < 0.001$; CV2 $\lambda = 0.1496$, $\chi^2 = 292.6$, d.f. = 54, $P < 0.001$; CV3 $\lambda = 0.5169$, $\chi^2 = 101.6$, d.f. = 26, $P < 0.001$). The projection of the individual scores onto the first two canonical variates (CV1 = 79%; CV2 = 15%) shows *D. auratus*, *D. brevirostris*, and *D. rhombeus* separated from *D. aureolus* along the first axis; CV2 separate *D. rhombeus* from *D. brevirostris* and *D. auratus* (Fig. 3).

An assignment test performed in the CVAGen6 program (Sheets 2004) determined that almost all *Diapterus* specimens were correctly assigned to one of the four species. On average, the percentage of correct assignment (CoAs) was >90%. Only two species, *D. aureolus* and *D. rhombeus*, had 100% PeCoAs.

Cohen-Kappa (κ) indicates that a PeCoAs of 28.9% would be expected by chance; the obtained value represents an improvement over chance of 93% ($\kappa = 0.933$; standard error = 0.023 confidence interval = 0.889 to 0.978; $z = 40.5$, $P < 0.001$). The *G*-test indicated that specimens were assigned to the correct species at rates significantly

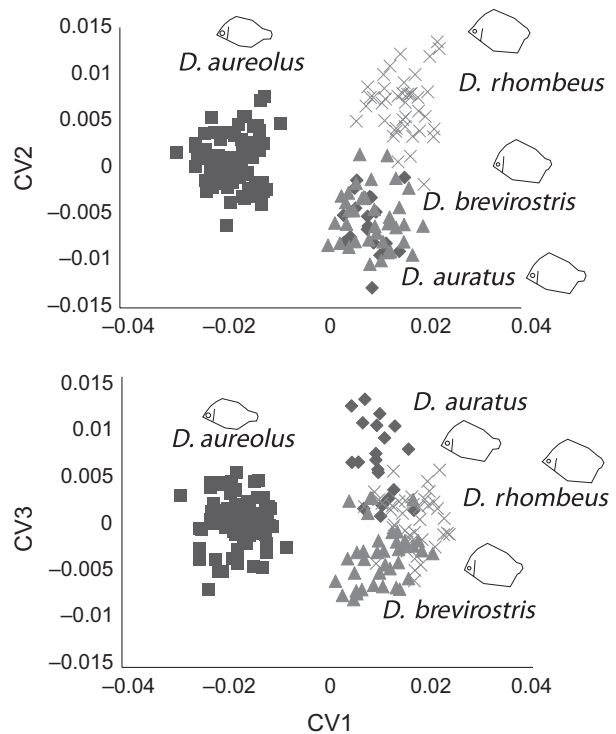


Fig. 3 Scatter plot generated with the canonical variables scores and the consensus shape of each species.

greater than would be expected by chance ($G = 386$; d.f. = 9, $P < 0.001$).

Phylogenetic reconstructions

Morphometric phylogeny. The maximum parsimony (MP) analysis, using the RWs, produced a single most parsimonious tree, with a consistency index (CI) = 0.50 and a retention index (RI) = 0.70 and tree length (TL) = 1.698. The topology recovers the monophyly of *Diapterus* with the Pacific species *D. brevirostris* and the Atlantic species *D. rhombeus* as sister taxa. The striped mojarra *Eugerres lineatus* is presented as the most akin of the outgroup species to *Diapterus* spp. (Fig. 4).

The maximum likelihood (ML) hypothesis shows a grouping pattern that does not recover the monophyly of *Diapterus*, leaving out *D. aureolus*. The tree suggests *D. rhombeus* and *D. brevirostris* as sister taxa and recovers *E. lineatus* nested within the *Diapterus* spp. in a clade consisting of *D. rhombeus*, *D. brevirostris* and *D. auratus* (Fig. 4).

Molecular phylogeny. A fragment of 2563 bp was constituted from 355, 415, 652 and 1141 bp from the 12SrRNA, 16SrRNA, COI and RAG1 genes, respectively. The fragment with the greater average number of variable sites was COI (27% of the length), followed by 16SrRNA (12.5%),

12SrRNA (11.3%) and RAG1 (4.9%). Substitution nucleotide models were the Tpm3+G+I for 12SrRNA, Tpm2+G+I for 16SrRNA, TrN+G for COI and HKY+G for RAG1.

The MP and BI trees recovered the same topology pointing to a close relationship between the most derived species, *D. rhombeus* and *D. brevirostris*, and the polyphyly of *Diapterus* by including *Eugerres plumieri* and excluding *D. aureolus* (Fig. 5).

Systematic accounts

Genus *Deckertichthys* Vergara-Solana, gen. N. (Family Gerreidae, Bleeker 1859).

Diapterus Ranzani 1842. Novi. Comment. Ac. Sci. Inst. Bonon., vol. 5, p. 340. Type, by original designation, *D. auratus* Ranzani.

Moharra Poey 1875. Enum. Pisc. Cub., p. 50. Type, by original designation, *Gerres rhombeus* Valenciennes.

Gerres Jordan & Gilbert 1882. Bull. U.S. Fish. Comm., vol. 1, p. 328. Type, by original designation, *Gerres aureolus* Jordan and Gilbert.

Diagnosis. A genus of mojarra, distinguished by the following characters: dorsal fins separated, notched to the base, the upper outline of spinous portion very oblique and with a prominent blotch on tip of membrane of anterior

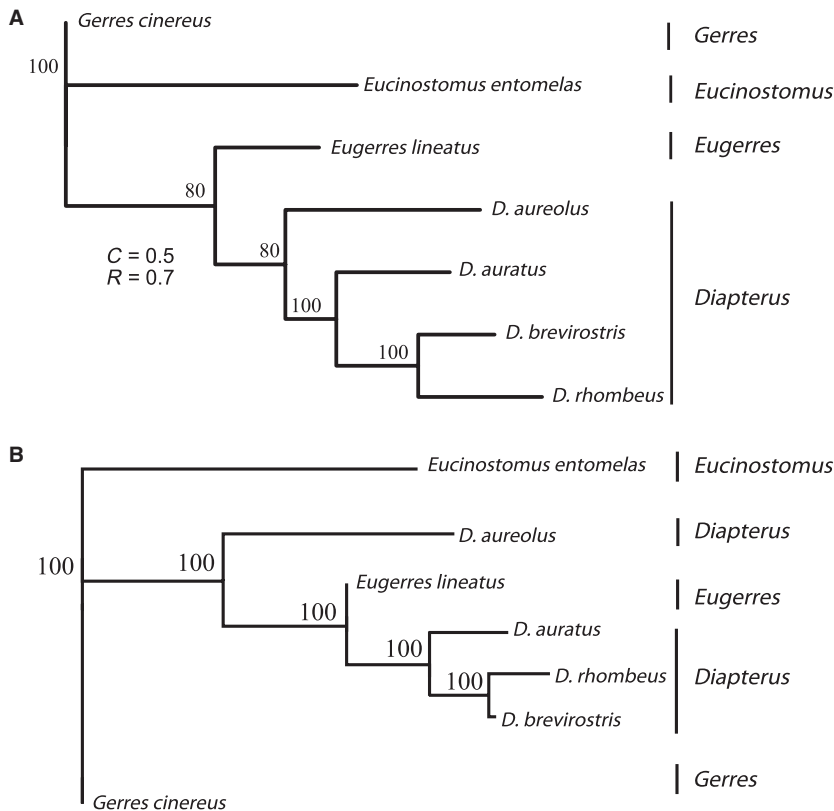


Fig. 4 —A. Tree generated from the relative warps (RWs) using maximum parsimony (MP). The consistency (C) and retention (R) indexes are shown. The jackknife monophyly index (JMI) is presented at each node. The sizes of the branches are relative to the number of steps. On the right side, species are grouped in their respective genus. —B. Tree generated from the RWs using maximum likelihood (ML). On the right side, species are grouped in their respective genus. The JMI is presented at node. On the right side, species are grouped in their respective genus.

spines. Dorsal spines 9, slender, very weak but slightly flexible, the second scarcely stronger than the third, 2.0 in length of head, 10 soft rays. Anal spines very short, 3, soft rays 8. Second and third anal spines subequal, 2.6 in length of head, second stronger than third. Preorbital entire, preopercle serrated. Body ovoid not rhomboidal, much compressed with the back elevated. The outline somewhat regularly elliptical, depth 2.25 in body length, outline along base of anal very oblique. Lateral line running high, everywhere much above axis of body, even on caudal peduncle. No distinct dark streaks along the rows of scales; 2.5 rows of scales between lateral line and dorsal fin, counted below base of first soft dorsal fin ray.

Etymology. *Deckertichthys* is named after Gary Dennis Deckert, from the combination of his surname and Latinized Greek, *ixthys*, *ichthys* (= fish); gender to be taken as neuter, singular. A tribute to G.D. Deckert, who first recognized the distinctiveness of this new taxon, and for his contribution to the study of Gerreidae.

Description. See description of species.

Type species.

Deckertichthys aureolus (Jordan & Gilbert 1882) by present designation.

Deckertichthys aureolus (Jordan & Gilbert 1882) comb. nov. (English name: golden mojarra; Spanish name: mojarra dorada) (Figure 6 and Table 1)

Gerres aureolus Jordan & Gilbert 1882. Bull. U.S. Fish. Comm., vol. 1, p. 328.

Diapterus aureolus Meek & Hildebrand 1925. Field Mus. Pub. No. 226, Zool. Ser. vol. 15, pt. 2, p. 594–595.

Type specimens

Neotype. CICIMAR-CI 8808; 105.4 mm SL, Pacific Ocean at Bahía Matanchén, Nayarit, Mexico; collected by J.T. Nieto-Navarro, on 15 December 2009. To preserve nomenclatural stability, here it is designated a neotype, according to Article 75 (75.3.1–75.3.7) of the Code (ICZN 1999), as no known types exist (see Remarks section) (Fig. 6).

Neoparatypes. CICIMAR-CI 8809 (54); 52.9–116.7 mm SL, Pacific Ocean at Bahía Matanchén, Nayarit, Mexico; collected by J.T. Nieto-Navarro, on 15 March 2010.

Additional material. See Material examined section.

Description. Based on 72 specimens, including the neotype, neoparatypes and additional material, the description

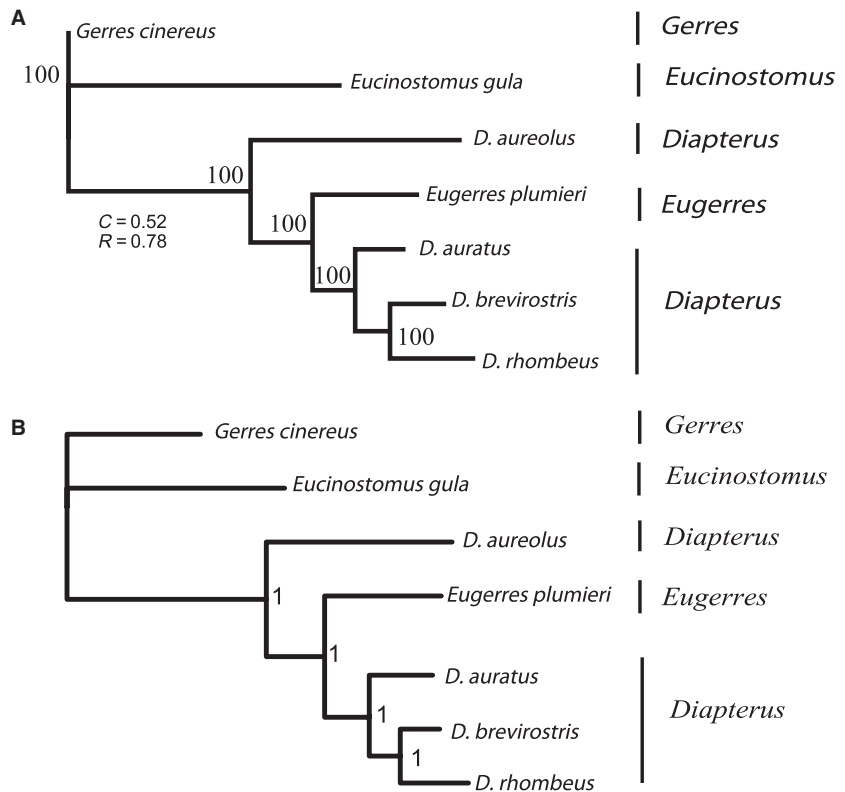


Fig. 5 —A. Tree generated from maximum parsimony criterion with the implicit enumeration algorithm using the DNA sequences. The consistency (C) and retention (R) indexes are shown. The jackknife monophyly index (JMI) is presented at each node. On the right side, species are grouped in their respective genus. —B. Graphic representation of the phylogenetic hypothesis generated with the molecular data using the Bayesian method, including the posterior probability values of the nodes. On the right side, species are grouped in their respective genus.

Table 1 Proportional measurements of specimens of *Deckertichthys aureolus* as percentages of the head length (HL) and standard length (SL), and meristic data for the type specimens

Character	All specimens					
	Neotype	n	Mean	Min	Max	SD
SL (mm)	105.40	70	84.9	52.9	116.7	11.6
TL (mm)	119.67	61	105.2	66.0	140.8	14.2
Head length (HL)	33.67	69	27.5	17.5	53.2	5.0
Peduncle width	14.48	70	11.0	6.4	17.0	2.1
Peduncle length	12.63	70	11.3	6.3	18.9	2.2
Percent of HL (%)						
Head height	94.4	68	109.1	89.01	129.4	7.2
Eye diameter	32.43	68	34.6	29.8	43.1	2.7
Snout length	16.30	66	19.9	14.4	25.4	2.6
Percent of SL (%)						
Dorsal fin length	46.24	70	50.3	45.0	56.3	2.1
Body depth at first anal spine	41.33	70	40.4	36.5	44.7	1.8
Predorsal length	42.16	70	43.8	40.0	47.5	1.4
Preanal length	66.98	70	67.0	61.2	74.0	2.4
Prepelvic length	42.87	70	39.5	34.9	48.1	2.1
Greatest body depth	43.87	70	43.3	37.4	48.6	2.3
Anal fin length	25.19	70	26.4	22.5	30.5	1.8
Length of the second anal spine	12.81	54	18.2	14.7	21.1	1.4
Counts						
	Neotype	Neoparatypes				
Pectoral fin rays	16	15–16				
Pored lateral line scales	32	31–34				
Scales above lateral	5	5				
Scales below lateral	9	8–9				
Gill rakers (upper) + (lower) =	–	7+ 11–13				

n = sample size; SD = standard deviation.

of Jordan and Gilbert (1882) and Deckert (1973) agrees very well with our specimens, formulated as (excluding that mentioned in the diagnosis of the genus): caudal peduncle very short and deep, tapering regularly to base of tail; snout rather pointed, the interorbital area strongly depressed. Maxillary long, reaching to a point midway between front and middle of pupil, the exposed portion narrowly oblong, its width about two-fifths its length; teeth slender, in narrow bands; groove on top of head for premaxillaries, scaleless, triangular, reaching a point opposite middle of eye, its width in front is two-thirds its length. Eye very large; its diameter greater than snout or interorbital width, 3% in head. Preopercle with the angle protracted, the margin sharply and finely serrated. Gill rakers very short, less than one-third diameter of pupil. Scales in about 4 rows on the cheek. Caudal fin deeply forked. Anal low; the second spine a little longer and noticeably stronger than the third, 2.2 times in head; soft rays posteriorly, not rising above their basal sheath of scales. Pelvic fins reaching well past vent, their length more than half of



Fig. 6 Neotype of *Deckertichthys aureolus* (Jordan & Gilbert 1882). CICIMAR-CI 8808; 105.4 mm SL, Pacific Ocean at Bahía Matanchen, Nayarit, Mexico. Collected in a shrimp trawl by J.T. Nieto-Navarro on 15 December 2009.

head. Pectorals fins long, as long as head, reaching slightly beyond origin of anal fin. Head 3.0 times in length; depth of body 2.4 times in length.

Comparisons. *Deckertichthys aureolus* differs from the other sympatric gerreid species in having dorsal fins separate, notched to the base, and spinous dorsal fin with a jet-black blotch on tip of membrane of anterior spines. The golden mojarra resembles *Eucinostomus* spp, but several differences, besides dorsal fin morphology, such as preopercle serrated, total numbers of spines and soft rays in the anal fin, and body depth (1.9–2.3 vs. 2.3–3.6, respectively), easily separate the two genera.

Colour in life and preservative. Silvery, darker above with bluish reflections, silvery below and sides with distinct tinge of pale yellow. Fins pale brownish yellow; vertical fins margined with black, spinous dorsal with a jet-black blotch on tip of membrane of anterior spines. Membrane of each spine and ray of dorsal with a distinct jet-black spot at its base. Ventral fins yellow on terminal portion of outer rays only and the very tips of these white. Tip of snout dark. Opercular membrane yellowish above. Lips with yellow tints; head yellowish silver.

Biology. There is not much knowledge of the biology of this species. They are found in coastal areas, but are very rare in coastal lagoons. These fish are commonly found in the discarded fauna of shrimp trawls.

Distribution. Coastal marine, not known to enter estuaries, *D. aureolus* is known from eastern tropical Pacific, from Bahía Magdalena in the State of Baja California Sur, Mexico (Arenas-Granados & Acero 1992), and off shore in

the Gulf of California from Bahía de San Luis Gonzaga in the State of Baja California to Puerto Pizarro, Peru (Allen & Robertson 1994; Amezcua-Linares, 1996).

Remarks. A situation that plays an important role in the taxonomic confusion of *Deckertichthys aureolus* (Jordan & Gilbert 1882) is the loss of the type specimen, which was collected by Charles H. Gilbert in the Panama Bay in 1881. This sample was held at the Smithsonian Natural History Museum under catalog number USNM 29487 (Eschmeyer & Fricke 2012); however, the type material is lost. The possible explanation that Deckert (1973) gives for the loss of this material, although anecdotal, is based on what was mentioned by David Starr Jordan in his autobiography [remarks in brackets]: On our return from Switzerland to Paris in September, was of my knowledge and my regret that Owen Hall, the old science building at the University of Indiana, was struck by lightning and burned almost everything together with its contents [in July 1883], including my valuable library and my collections, and a manuscript of a considerable volume of Jordan and Gilbert of fishes of the west coast of Mexico and Panamá [‘The fishes of the Pacific coast of tropical America’, never rewritten or published]. Along with the book also the samples in which this was based were lost. Most of these samples were not replaced until I realized an expedition to Mazatlan in 1895 and another by Gilbert and Starks to Panama in 1903. Hubbs (1964) mentioned that large fish collections from one trip to Mazatlán [Sinaloa, Mexico] in 1881, and two trips to Panama in 1882 by C.H. Gilbert, were part of the material destroyed in the fire [the Science Hall at Seminary Square, at Indiana University]. Because *Deckertichthys aureolus* (= *Gerres aureolus*) was described in 1882 from a single specimen collected in Panama by C.H. Gilbert between February and March of 1881 [for the United States National Museum], we believe that it was destroyed in the fire mentioned by D.S. Jordan.

Material examined

Specimens representing juveniles and adults of *Deckertichthys aureolus* and related species are preserved in alcohol and mainly deposited at CICIMAR-CI. Materials are arranged alphabetically by genus and species, followed by sample localities, museums or institutional collections, and their record numbers, sample size (in parentheses) and standard length (SL) in mm [square brackets]; n/n = no catalog numbers. Institutional abbreviations are listed in <http://www.asih.org/codons.pdf>; an additional institution is abbreviated: CICIMAR-CI (Centro Interdisciplinario de Ciencias Marinas, Ichthyological Collection, La Paz, Baja California Sur, Mexico). Fish and tissue samples are available upon request (<http://coleccion.cicimar.ipn.mx>).

Diapterus auratus. Vitoria Santa Cruz, Brazil: CAS (SU) 61814 (1) [108.5]. Fortaleza, Mucuripe, Brazil: CAS (SU) 52257 (1) [74.7]. Indian River, Florida, USA: UF 89792 (76) [20.8–42.9]. Melbourne Beach, Florida, USA: AMNH 56041 (2) [47–57]. Collier, Florida, USA: UF 74616 (1) [176.6]. Sewell’s Point, Florida, USA: AMNH 21823 (3) [22–61]. Pamlico River, North Carolina, USA: UF 25550 (1) [223.0].

Diapterus rhombeus. Santo Domingo, Dominican Republic: AMNH 15080 (2) [53 – 54]. Haiti: AMNH 224760 (225) [87 – 88]. Port Prince, Haiti: AMNH 37125 (7) [22 – 61]. Havana, Cuba: SU1964 (1) [85.4]. Caribbean Sea, Jamaica: CAS (SU) 4811 (1) [91.8]. Natal, Rio Grande Do Norte, Brazil: AMNH 3852 (3) [81 – 85]. Lago Papary, Rio Grande Do Norte, Brazil: CAS (SU) 22091 (1) [96.9]. Salvador, Punta de Nuestra Señora, Bahía, Brazil: CAS (SU) 68145 (1) [95.7]. Bahía de Amatique, Puerto Barrios, Izabal, Guatemala: AMNH 35189 (24) [40 – 44].

Diapterus brevirostris. CICIMAR-CI 2090 (1) [117]. Bahía Concepción, Baja California Sur, Mexico, CICIMAR-CI 2707 (1) [150]. Bahía Magdalena, Baja California Sur, Mexico, CICIMAR-CI 1673 (1) [117]. (2) [95.5 – 99.89]. El Conchalito, La Paz, Baja California Sur, Mexico: CICIMAR-CI 6000 (9) [19 – 30]. El Conchalito, La Paz, Baja California Sur, Mexico: CICIMAR-CI 5427 (8) [26 – 41]. El Conchalito, La Paz, Baja California Sur, Mexico: CICIMAR-CI 6006 (31) [32 – 88]. El Conchalito, La Paz, Baja California Sur, Mexico: CICIMAR-CI 5456 (5) [53 – 63]. Estero Las Botellas, Bahía Magdalena, Baja California Sur, Mexico: CICIMAR-CI 3086 (2) [126 – 134]. Playa Santispac, Bahía Concepción, Baja California Sur, Mexico: CICIMAR-CI 2707 (1) [146]. Ensenada de La Paz, Baja California Sur, Mexico: CICIMAR-CI 1686 (1) [143]. Playa Santispac, Bahía Concepción, Baja California Sur, Mexico: CICIMAR-CI 2747 (1) [150]. Puerto San Carlos, Baja California Sur, Mexico: CICIMAR-CI 3092 (1) [133]. Puerto San Carlos, Baja California Sur, Mexico. CICIMAR-CI 1320 (3) [131 – 144]. Shrimp pond, Centro de Investigaciones Biológicas del Noroeste (CIBNOR), Ensenada de La Paz, Baja California Sur, Mexico. CICIMAR-CI 5963 (18) [127 – 148]. Ensenada de La Paz, Baja California Sur, Mexico. CICIMAR-CI 590 (3) [117 – 120].

Deckerichthys aureolus. Bahía de Matanchén, Nayarit, Mexico: CICIMAR-CI 8808 (1) [105.4]. Bahía de Matanchén, Nayarit, Mexico: CICIMAR-CI 8809 (54) [52.9 – 116.7]. San Mateo del Mar, Oaxaca, Mexico: EMU – PI358 EMUPI358 (2) [52 – 53]. Buenaventura, Colombia: CICIMAR-CI n/n (7) [82.6 – 93.8]. Punta Arenas, Golfo de Nicoya, Costa Rica: UCR23633.004 (2) [74 – 81]. Bahía

de San Luis Gonzaga, Baja California, Mexico: EMUPI354 (5) [64 – 73]. Bahía Almejas, Baja California Sur, Mexico: IBUNAMP5798 (1) [79].

Identification key to the genera and species of Gerreidae treated in this article

- 1a. Margin of preopercle serrated, anal fin elements (spines and soft rays) 11, body ovate or rhomboid, the depth 1.9–2.3 in standard length2
- 1b. Margin of preopercle smooth, anal fin elements (spines and soft rays) 10, body slender, oblong or deep, the depth 2.2–3.3 in standard length 6
- 2a. Preorbital bone smooth, body without dark lengthwise stripes3
- 2b. Preorbital bone serrated except in very young (< 50 mm standard length) sides of body with black longitudinal stripes8
- 3a. Body ovate, the outlines somewhat regularly elliptical, the depth a little less than half length, dorsal fins separate, the upper outline of spinous portion very oblique, and with a prominent blotch on tip of membrane of anterior spines. Ranged: Eastern Pacific.....*Deckertichthys aureolus*
- 3b. Body rhomboid, short and deep, the depth usually rather more than half of SL, dorsal fins not separate, rather deeply notched to the base, and without a prominent blotch on tip of membrane of anterior spines4
- 4a. Anal-fin rays typically with two spines and nine soft rays, gill rakers on lower limb of first gill arch 16–18, usually 17. Range: Western Atlantic*Diapterus rbombeus*
- 4b. Anal-fin rays typically with three spines and eight soft rays or with two spines, one unbranched ray, and 8 branched soft rays in small specimens (< 50 mm standard length), gill rakers on lower limb of first gill arch 10–15 5
- 5a. Dorsal fin deeply notched, second anal spine 1.6 times in head length, body depth 1.7 to 2.4 times in standard length, number of gill rakers on lower limb of first gill arch 12 to 15, usually 12 or 13. Range: Western Atlantic*Diapterus auratus*
- 5b. Dorsal fin not deeply notched, second anal spine 1.8 in head length, body depth 1.9–2.0 times in standard length, number of gill rakers on lower limb of first gill arch 12–15. Range: Eastern Pacific*Diapterus brevirostris*
- 6a. Body deep, the depth 2.2–2.6 in standard length, pelvic fins yellow, sides of body with 6 or 7 obscure bars. Range: on both coasts of America *Gerres cinereus*

6b. Body oblong to moderately deep, the depth 2.4–3.3 times in standard length, sides of body without obscure bars 7

7a. Body deep, 2.0–2.4 times in standard length, scaleless pit of premaxillary groove crossed anteriorly by row of scales, without a prominent dark blotch at the upper end of branchial chamber. Range: Western Atlantic*Eucinostomus gula*

7b. Body slender, 2.5–2.8 times in standard length, scaleless pit of premaxillary groove not crossed anteriorly by row of scales, with a prominent dark blotch at the upper end of branchial chamber. Range: Eastern Pacific *Eucinostomus entomelas*

8a. Lateral stripes very distinct, 12 or 13 in number, maxilla usually extending to or beyond the anterior margin of pupil. Range: Western Atlantic *Eugerres plumieri*

8b. Lateral stripes very distinct, 9 or 10 in number, maxilla usually not extending beyond the anterior margin of pupil. Range: Eastern Pacific *Eugerres lineatus*

Discussion

Comparisons between the consensus shape of each species suggested that the most important difference in shape among *Diapterus* species consists of a more rhomboidal body, except for *D. aureolus* (Fig. 3). The CDA indicates that shapes of the four species were statistically different (Table 2). Moreover, comparisons of geometric morphometric analyses of body shape revealed a clear distinction between *Deckertichthys aureolus* and species of *Diapterus*, an interpretation that is consistent with the phylogenetic analysis.

In this sense, to maintain monophyletic groups and correspondence with molecular and morphometric data, removal of *Diapterus aureolus* (Jordan & Gilbert 1882) from remaining *Diapterus* creating a new monotypic genus is needed. This solution is also supported by morphological and ecological information that was independently generated (e.g. Deckert 1973; Álvarez-Pliego 2010; Vergara-Solana et al. 2013).

The phylogenetic hypothesis, based on morphometric and molecular data, suggests that *Deckertichthys aureolus* is not sister to the species of *Diapterus*. The sibling species, *D. brevirostris* and *D. rbombeus*, are distributed in separate basins, which suggests that speciation within this genus in the Neotropics occurred before the final rise of the Panamanian Isthmus about 3.2 million years ago (Jackson et al. 1996a,b; Coates et al. 2004; Bartoli et al. 2005).

The polyphyly of *Diapterus* was suggested by all generated trees, with the exception of the result found from morphometric data using maximum parsimony algorithm. This is related to differences in the methods and not the data. The jackknife monophyly index (JMI) also supports

Table 2 Specimen classification according to the discriminant model including the percentage of correct assignment (PeCoAs)

	<i>Diapterus auratus</i>	<i>Deckertichthys aureolus</i>	<i>Diapterus brevirostris</i>	<i>Diapterus rhombeus</i>	PeCoAs, %
<i>D. auratus</i>	17	0	2	1	85.0
<i>D. aureolus</i>	0	72	0	0	100.0
<i>D. brevirostris</i>	4	0	33	1	86.8
<i>D. rhombeus</i>	0	0	0	40	100.0
				Overall mean	93.0

this conclusion, as the tree found from morphometric data, using maximum parsimony, also had the lowest support value.

As noted here, our phylogenetic proposal suggests that *Diapterus* is not monophyletic. If the classification of these fish is to be consistent with their evolutionary history, monophyly is required. Given the phylogenetic evidence, there are two taxonomic and nomenclatural classification scenarios: (i) Remove *Eugerres* and put all these species into *Diapterus* (e.g. Andreata 1988; Miller 2005) or (ii) exclude *Diapterus aureolus* (*sensu lato*) from *Diapterus* spp. leaving the former as a monophyletic group which require defining a new genus. There is enough morphological, osteological, ecological and molecular evidence to reject the first option (e.g. Deckert 1973; Deckert & Greenfield 1987; Bianchi 1991; Castro-Aguirre *et al.* 1999; López-Peralta & Arcila 2002; Ruiz-Carus & Uribe-Alcocer 2003a, b; Díaz-Ruiz *et al.* 2006; Chen *et al.* 2007; De La Cruz-Agüero & Chollet-Villalpando 2012; De La Cruz-Agüero *et al.* 2012).

The former misperceptions about the relative position of *Deckertichthys aureolus* is related in part to the loss of the type specimen with no type series defined (an example of a singleton *sensu* Lim *et al.* (2012): species descriptions based on a single specimen), together with the unpublished results of G. D. Deckert, concerning the designation of the new taxon (Deckert 1973; Deckert & Greenfield 1987). The same scenario occurred in this family, with the unpublished theses written by Curran (1942) for the genus *Lepidochir* and two species of the genus *Eucinostomus* by Zahuranec (1967).

In our study, the results from morphological information of all species, as well as the phylogenetic hypotheses generated independently using characters of diverse nature and two methodologically different strategies, provide conclusive evidence to support the generic separation of *Diapterus aureolus* (*s.l.*), despite the monotypy of the construction from the genus *Diapterus* and its placement in a new combination, *Deckertichthys aureolus* (Jordan & Gilbert 1882). We believe that our results are sufficiently robust to support the new taxonomic arrangement, considered an important step towards a better understanding of the natural history and systematics of the group.

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