Phylogenetic position and notes on the natural history of *Pimelabditus moli* Parisi & Lundberg, 2009 (Teleostei: Siluriformes), a recently discovered pimelodid catfish from the Maroni River basin

by

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ABSTRACT. - The recent description of a distinctive new pimelodid catfish, *Pimelabditus moli* Parisi & Lundberg, 2009, from the Maroni River basin of Suriname and French Guiana, added an unresolved taxon to the family. Here we include *P. moli* in ongoing molecular and morphological phylogenetic studies of the Pimelodidae. We sequenced > 7.5 KB of aligned bases from the nuclear *rag1* and *rag2* genes and the mitochondrial *mt-rnr1*, *mt-rnr2* and *mt-cyb* genes. Results provide strong support for the placement of *P. moli* as the sister taxon to *Pimelodus ornatus* Kner, 1858. We also describe a structurally complex pterotic-epioccipital fossa shared by *P. moli* and *P. ornatus* that provides an unambiguous synapomorphy indicating their close relationship. Furthermore, the molecular and morphological data recover the *P. moli -P. ornatus* Clade as the sister group to the *Calophysus-Pimelodus* Clade. *Pimelabditus moli* is a rare species, known from just five specimens. Notes on the provenance, capture and habitat of *P. moli* are provided.

RÉSUMÉ. - Placement phylogénétique et notes sur l'histoire naturelle de *Pimelabditus moli* Parisi & Lundberg, 2009 (Teleostei : Siluriformes), un poisson-chat pimélodidé récemment découvert du bassin du fleuve Maroni.

La description récente d'un poisson-chat pimélodidé nouveau et particulier, *Pimelabditus moli* Parisi & Lundberg, 2009, des versants surinamais et guyanais du fleuve Maroni, a mis en évidence un taxon dont la position phylogénétique n'est pas résolue. Nous incluons ici *P. moli* au sein d'une étude phylogénétique moléculaire et morphologique des Pimelodidae actuellement en cours. Nous avons séquencé et aligné plus de 7500 bases issues des gènes nucléaires *rag1* et *rag2* et des gènes mitochondriaux *mt-rnr1*, *mt-rnr2* et *mt-cyb*. Les résultats soutiennent fortement la position de *P. moli* en tant que groupe frère de *Pimelodus ornatus* Kner, 1858. Nous décrivons également une fosse ptérotique-épioccipitale de structure complexe commune à *P. moli* et *P. ornatus*, qui fournit sans ambiguïté une synapomorphie indiquant leur proche parenté. De plus, les données moléculaires et morphologiques retrouvent le clade *P. moli -P. ornatus* en tant que groupe frère du clade *Calophysus-Pimelodus*. *Pimelabditus moli* est une espèce rare uniquement connue de cinq spécimens. Des informations concernant la provenance, la capture et l'habitat de *P. moli* sont fournies.

Key words. - Pimelodidae - French Guiana - Suriname - Neotropics - Molecular systematics - Osteology.

With over 100 valid species and several more known yet unnamed, the Pimelodidae is a moderately species rich family of Neotropical catfishes (Lundberg and Littmann, 2003). Pimelodids display a remarkable diversity of body sizes and forms, colours and pigmentation patterns, and natural histories. These catfishes are abundant and diverse in all large cis-Andean watersheds from the Orinoco to the La Plata-Paraná. Pimelodids are present, but less diverse, in the rivers across the Caribbean slope of northern South America westward from the Maracaibo to the Atrato basins, and in the Tuyra River on the Pacific slope of lowermost Panama.

The rivers of the Guianas flowing into the Atlantic have been long explored by ichthyologists. Nevertheless, discoveries continue with about 100 newly described fish species found in the region since 1980 (Vari and Ferraris, 2009). Eighteen pimelodid species were recently listed from the Guianas (Lundberg, 2009), and, most recently, *Pimelabditus moli* Parisi & Lundberg, 2009 was added as a new genus and species of the family Pimelodidae from the Maroni River, the largest drainage basin in the Guianas ecoregion as defined by Abell *et al*. (2008). The Maroni basin occupies an area of around 65,000 to 69,000 km^2 in the eastern part of

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Suriname and western part of French Guiana, and its mainstem is 720-km-long (Ziesler and Ardizzone, 1979; Amatali, 1993; Meunier *et al*., 1998). Its ichthyofauna totals 305 species (Mol *et al*., 2012), and is characterized by a high level of endemism relative to species richness (Meunier *et al*., 1998). In this context, *P. moli* represents an intriguing species.

Pimelabditus moli possesses extraordinary diagnostic features of its cranial skeleton and dentition that set it apart from other pimelodids (Parisi and Lundberg, 2009). With that description, a first phylogenetic evaluation of *Pimelabditus* using morphological characters firmly established this catfish as a member of Pimelodidae and placed it above the phyletically deep genera *Steindachneridion*, *Phractocephalus* and *Liearius* in a large clade containing all other pimelodids. However, with available morphological data the relationships of the new catfish were not more precisely resolved.

Thus, as a divergent, narrowly endemic and unresolved pimelodid lineage, *P. moli* has an uncertain history and implication for the assembly of the Guianan fish biota. To address these questions we added *P. moli* to a continuing investigation of pimelodid phylogeny and biogeography using nuclear and mitochondrial gene sequences (Sullivan *et al*., pers. data; Lundberg *et al*., 2011). Also, one of us (JGL) has further examined the skeletal anatomy of *P. moli* in comparison to other pimelodids and remaining pimelodoids (i.e., Heptapteridae, Pseudopimelodidae and *Conorhynchos*) for potentially informative characteristics. In this paper we report the results of these studies, present additional information on the habitat of *P. moli* and comment on the fish fauna of the Maroni system.

MATERIALS AND METHODS

Molecular dataset: markers and taxon sample

Sequences of the nuclear *recombination activating gene 1* (*rag1*) and *recombination activating gene 2* (*rag2*) genes, and mitochondrial *16S RNA* (*mt-rnr1*) and most of the *12S RNA* (*mt-rnr2*) genes were obtained from three specimens of *P. moli* by coauthor R. Covain. Naming of the different genes follows recommendations from the Zebrafish Nomenclature Committee (Sprague *et al*., 2006; Zebrafish Model Organism Database (ZFIN), University of Oregon, Eugene, OR 97403-5274; URL: http://zfin.org/zf_info/nomen.html), and acronyms for institutions follow Sabaj Pérez (2010).

The data from one paratype specimen (ANSP 188900) were not included in this study because its sequence of *rag1* did not amplify. The *rag1*, *rag2*, *mt-rnr1* and *mt-rnr2* sequences of the other two *P. moli* individuals (holotype MHNG 2709.100, paratype MHNG 2709.099) were added to the existing molecular sequence dataset for Pimelodidae previously assembled by coauthor J. Sullivan (Lundberg *et al*., 2011).

The full pimelodid dataset contains 7,583 aligned bases of nuclear *rag1* and *rag2* genes (3607 bases), mitochondrial *mt-rnr1* and *mt-rnr2* genes (~2720 bases), and *mt-cyb* genes (1137 bases) plus 117 bases of the trailing *tRNA valine* (*mt-tv*). The *mt-cyb*/*tRNAval* sequences were not obtained for *P. moli*. In addition to the new *P. moli* sequences, our data set includes two outgroup species (the heptapterid *Goeldiella eques* and the pseudopimelodid *Pseudopimelodus mangurus*), and 78 pimelodid ingroup specimens as terminals representing 27 of the family's 31 named genera plus one undescribed genus, and 54 named plus as many as 10 undescribed species (Tab. I herein; Lundberg *et al*., 2011).

GenBank accession numbers for the three *P. moli* nucleotide sequences are:

MHNG 2709.100: *rag1* JF489900 *rag2* JF489903, *mt-rnr1*/*mt-rnr2* JF489897, MHNG 2709.099: *rag1* JF489901, *rag2* JF489905, *mt-rnr1*/*mt-rnr2* JF489899, ANSP 188900: *rag1* (exon 3) JF489902, *rag2* JF489904, *mt-rnr1*/*mt-rnr2* JF489898. GenBank accession numbers and specimen data for the other pimelodid specimens are available in Lundberg *et al*. (2011).

Sequence alignment

For the *rag* partition, we excluded the first intron in *rag1* from our analyses since significant length variation (between 155 and 675 base pairs among pimelodoids) made alignment impractical. We aligned the coding sequences of the *rag* fragments using the software RevTrans 1.4 (Wernersson and Pedersen, 2003) that translates the sequences, determines an amino acid alignment, and then backfills the DNA sequence. Indels are relatively few in the *rag* sequence alignments and only a small fraction of the *rag* sites presented any alignment ambiguity once codon positions are taken into account. For the noncoding mitochondrial genes, a conservative approach assuming that confidence in homology assessment within a column of aligned characters increases with stability of this assessment to perturbation of alignment parameters (Löytynoja and Milinkovitch, 2001), we performed two alignments in ClustalX v.1.8.3.1 (Thompson *et al*., 1997): the first with the default values for gap opening/gap extension of 15/6.66 and a second with relaxed gap extension parameter of 15/0.02. We designated sites that shifted their alignment to be ambiguously aligned and we removed these from all analyses.

Phylogenetic analyses, maximum likelihood

We conducted likelihood analyses of the complete dataset in RAxML 7.2.6 (Stamatakis, 2006, 2008) using five data partitions: one for each *rag* codon position, one for the *cytb*/tRNAval data, and another for the 12S/16S block. AIC scores calculated in MrModelTest 2.2 (Nylander, 2004) favoured

Table I. - Genera and species of Pimelodidae sampled in this and previous phylogenetic studies. Specimens examined in previous morphological studies are listed in the references indicated by footnotes to genera. Specimens newly examined for morphological features are tabulated here. Abbreviations: Institutional acronyms follow Sabaj Pérez (2010); CS, cleared and stained skeletal preparation. a, Aguilera *et al*., 2008; b, Azpelicueta *et al*., 2008; c, Buitrago-Suárez, 2006; d, Buitrago-Suárez and Burr, 2007; e, Figueiredo and Carvalho, 1999a; f. Figueiredo and Carvalho, 1999b; g, Garavello, 2005; h, Howes, 1983; i. Lucena *et al*., 1992; j, Lundberg *et al*., 1991; k, Lundberg and Parisi, 2002; l, Lundberg and Aguilera, 2003; m, Lundberg and Akama, 2005; n, Lundberg and Dahdul, 2008; o, Nass, 1991; p, Parisi *et al*., 2006; q, Parisi and Lundberg, 2009; r, Rocha *et al*., 2007; s, Sabaj-Pérez *et al*., 2007; t, Stewart, 1986; u, Stewart and Pavlik, 1985.

Genus	Species: molecular	Species and newly examined specimens: morphology
Aguarunichthys [t]	*A. inpai*	*A. torosus*, MZUSP 50398, 1, CATSCAN http://catfishbone.ansp.org/
Bagropsis	–	*B. reinhardti*, MZUSP 39671, 1, CS
Bergiaria	–	*B. westermani*, ANSP 172139, 3, Xray, MZUSP 85627, 3, Dry skeleton
Brachyplatystoma [c, j, m, o]	*B. capapretum* *B. filamentosum* *B. juruense* *B. platynemum* *B. rousseauxii* *B. tigrinum* *B. vaillantii*	*B. capapretum* *B. filamentosum*, ANSP 187105, 1, Dry skeleton *B. juruense* *B. platynemum* *B. rousseauxii*, ANSP 187109, 1, Dry skeleton *B. tigrinum* *B. vaillantii*, ANSP 187107, 1, Dry skeleton
Calophysus [j, k, o, t]	*C. macropterus*	*C. macropterus*
Cheirocerus [b, j, k, u]	*C. abuelo* *C. eques* –	*C. abuelo* *C. eques* *C. goeldi*
Duopalatinus [j, k]	– *D. peruanus*	*D. emarginatus*, MZUSP 85622, 1, Dry skeleton, MZUSP 39671, 1 CS, 2 Xray *D. peruanus*
Exallodontus [j, k]	*E. aguanai*	*E. aguanai*
Hemisorubim [c, j, k, o]	*H. platyrhynchos*	*H. platyrhynchos*
Hypophthalmus [h, j, k]	*H.* cf. *edentatus* *H. fimbriatus* *H.* cf. *marginatus*	*H.* cf. *edentatus*, ANSP 178511, 2, Dry skeleton *H. fimbriatus* *H.* cf. *marginatus*, ANSP 178512, 7, Dry skeleton
Iheringichthys [j, k]	*I. labrosus*	*I. labrosus*, MZUSP 78459, 1, Dry Skeleton
Leiarius [j, k, o]	*L. marmoratus* *L. pictus*	*L. marmoratus* *L. pictus*
Luciopimelodus [t]	*L. pati*	*L. pati* ANSP 178798, 1, Dry skeleton
Megalonema [j, k, n, o, t]	*M. platanum* *M. platycephalum* *M. psammium* *M. amaxanthum* *M. orixanthum* *M. xanthum*	*M. platanum* *M. platycephalum* *M. psammium* *M. amaxanthum* *M. orixanthum* *M. xanthum*
Parapimelodus [i, j]	*P. nigribarbis* *P. valenciennis*	*P. nigribarbis* *P. valenciennis*, ANSP 178800, 1, Dry skeleton
Perrunichthys [a]	*P. perruno*	*P. perruno*, MBUCV L18, L19-2001, 2, Dry skeleton
Phractocephalus [a, j, l, o]	*P. hemioliopterus* – –	*P. hemioliopterus* †*P. acreornatus* †*P. nassi*
Pimelabditus [q]	*P. moli*	*P. moli*
Pimelodina [a, j, k, t]	*P. flavipinnis*	*P. flavipinnis*

GTR+G+I models for each partition, however since parameters G and I are strongly correlated and unidentifiable for small values of α, and because G accommodates for the absence of I (Kelchner and Thomas, 2006), we assigned a GTR+G model to each partition. We ran the analysis three times from random starting trees, and performed rapid bootstrapping with 1000 pseudoreplicates using the "GTRCAT" approximation.

Parsimony analysis

We analysed the nuclear and mitochondrial data combined and separately with maximum parsimony (MP) in PAUP*4.0b10 (Swofford, 2002). For each parsimony analysis we performed a heuristic tree search using the tree bisection-reconnection algorithm in which we obtained starting trees by stepwise addition using a random addition sequence for 1,000 replicates. In these searches we treated gaps (indels) as

Table I. - Continued.

Genus	Species: molecular	Species and newly examined specimens: morphology
Pimelodus [b, j, k, o]	*P. albicans*	*P. albicans*, ANSP 178802, 2, Dry skeleton
	–	*Pimelodus absconditus*
	–	*P. albofasciatus*
	–	*P. altissimus*, ANSP 178519, 1, Dry skeleton
	P. cf. *altissimus* n. sp.	*P. cf. altissimus* n. sp.
	P. argenteus	*P. argenteus*, ANSP 181017, 1, Dry skeleton
	P. blochii	*P. blochii*
	P. cf. *blochii*	–
	P. coprophagus	*P. coprophagus*, MBUCV L05-2001, 1, Dry skeleton
	–	*P. fur*, MZUSP 85477, 3, Dry skeleton
	–	*P. grosskopfii*
	–	*Pimelodus heraldoi*
	–	*P. jivaro*
	P. maculatus	*P. maculatus*
	–	*Pimelodus mysteriosus*, ANSP 180506, 1, Dry skeleton
	P. ornatus	*P. ornatus*, ANSP 178452, 1, Dry skeleton, ANSP 180985, 1, Dry skeleton
	P. pictus	*P. pictus*
	–	*P. pintado*
	–	*Pimelodus platicirris*
Pinirampus [j, k, t]	*P. pirinampu*	*P. pirinampu*
Platynematichthys [j, k, o]	*P. notatus*	*P. notatus*
Platysilurus [j, k, o, s]	*P. malarmo*	*P. malarmo*, MBUCV L17-2001, 1, Dry skeleton
	P. mucosus	*P. mucosus*
Platystomatichthys [j, s, k, o]	*P. sturio*	*P. sturio*
Propimelodus [k, p, r]	–	*P. eigenmanni*
	–	*P. caesius*
	–	*P. araguayae*
	P. n. sp. AM 1	*P.* n. sp. 1, ANSP 178518, 1, Dry skeleton
	P. n. sp. AM 2	*P.* n. sp. 2, ANSP 180939, 1, Dry skeleton
	P. n. sp. OR	*P.* n. sp. OR, ANSP HLR 79-004
Pseudoplatystoma [j, c, d, k, o, s]	*P. corruscans*	*P. corruscans*, MZUSP 78477, 2, Dry skeleton
	P. fasciatum	*P. fasciatum*
	P. magdaleniatum	*P. magdaleniatum*
	P. tigrinum	*P. tigrinum*
Sorubim [c, j, o]	*S. cuspicaudus*	*S. cuspicaudus*, MBUCV L21-2001, 1, Dry skeleton
	S. elongatus	*S. elongatus*
	S. lima	*S. lima*
	S. maniradii	*S. maniradii*
Sorubimichthys [c, j, k, o]	*S. planiceps*	*S. planiceps*
Steindachneridion [e, f, g, j]	*S. scriptum*	*S. scriptum*, MZUSP 78463, 1, Dry skeleton
	–	†*Steindachneridion iheringi*, DGM 16-P, 1, Latex cast
	–	†*Steindachneridion silvasantosi*, DGM 1291-P, 1, Latex cast
Zungaro [c, j, k, o]	*Z. zungaro*	*Z. zungaro*
Undescribed	Pimelodidae n. sp.	Pimelodidae n. sp., ANSP AMZ 96-025, CS

"missing" not as a fifth state, and all characters and character-state transformations were unweighed. We estimated branch support in parsimony for the combined and separate datasets with the non-parametric bootstrap procedure (Felsenstein, 1985) using 1,000 replicates with 10 random-addition replicates each. Also, we determined decay (Bremer) support values for the partitioned nuclear and mitochondrial data for nodes in the MP trees using TreeRot 2 (Sorenson, 1999).

Morphology

Coauthor Lundberg compared *P. moli* to specimens representing all other valid pimelodid genera (Tab. I) for phylogenetically informative skeletal characters. Newly examined specimens and references to work containing lists of previously examined specimens are given in table I. Visualization of the skeleton of *P. moli* used digital radiographs of the holotype and two paratypes taken at ANSP, and a 25 μm resolution CTscan of ANSP 188900 made at the Micro-CT Imaging Facility at Cornell University's Department of Biomedical Engineering. The CT images of the skeleton created for this paper were produced by K. Luckenbill at ANSP with the software package VG Studio Max® and Adobe®Photoshop®CS. Comparative skeletal material of Pimelodidae (Tab. I) is mainly housed at ANSP and includes dry and cleared/stained skeletal preparations, additional high-resolution CTscan and 2D radiographic images.

Anatomical terminology, as far as possible, follows the Teleost Anatomical Ontology, TAO (Dahdul *et al*. 2010; www. obofoundry.org/cgi-bin/detail.cgi?id=teleost_anatomy).

RESULTS

Molecular dataset characteristics

The nuclear *rag1* and *rag2* partition consists of 3,607 characters of which 2,331 are constant and 812 are informative for parsimony. We found 221 characters of the mitochondrial *mt-rnr1* and *mt-rnr2* sequences to be ambiguously aligned and removed these from the analyses. The remainder of mitochondrial partition has 3,755 aligned characters of which 2,375 are constant and 1,105 are parsimony-informative.

Phylogenetic results of combined data analyses

The best Maximum Likihood tree found in the three RAxML analyses using the combined data has a log likelihood (LnL) = -59713.18. Figure 1 shows the resolved backbone of this tree emphasizing the nodes near and below *P. moli* with their ML bootstrap proportions at or above 50%.

The combined-data Maximum Parsimony analysis yields eight most parsimonious trees of 9,920 steps and a Consistency Index of 0.314 with uninformative characters excluded. The strict consensus topology of the 8 MP trees matches the ML topology except for the position of *Phractocephalus* and the unresolved "sorubimines" as indicated by dashed branch lines in figure 1. The MP bootstrap proportions at or above 50% and the partitioned decay values for the nodes of interest are also shown in figure 1.

Focusing on the phylogenetic placement of *P. moli* among the major groups of Pimelodidae, both ML and MP analyses of the combined data unequivocally recover a *P. moli -P. ornatus* Clade with bootstrap values of 100 and high positive decay values for both the nuclear and mitochondrial data partitions. In this topology *P. ornatus* stands apart from other terminals currently placed in the genus *Pimelodus* (type species *P. maculatus*). Our sample of *P. ornatus* includes four specimens of this widely ranging species or species complex, one each from the Essequibo, Orinoco, Amazon and Paraná.

The ML and MP combined-data analyses place the *P. moli -P. ornatus* Clade in a large monophyletic group here designated the OCP Clade, that also includes the *Calophysus* Group and *Pimelodus* Group of Lundberg *et al*. (1991). Both the *Calophysus* Group and *Pimelodus* Group are well supported as monophyletic. Further, the *Calophysus* Group and *Pimelodus* Group are recovered as sister taxa in a lineage named the *Calophysus-Pimelodus* Clade by Lundberg *et al*. (1991) and here abbreviated the CP Clade. Although the CP Clade is positively supported by the combined molecular

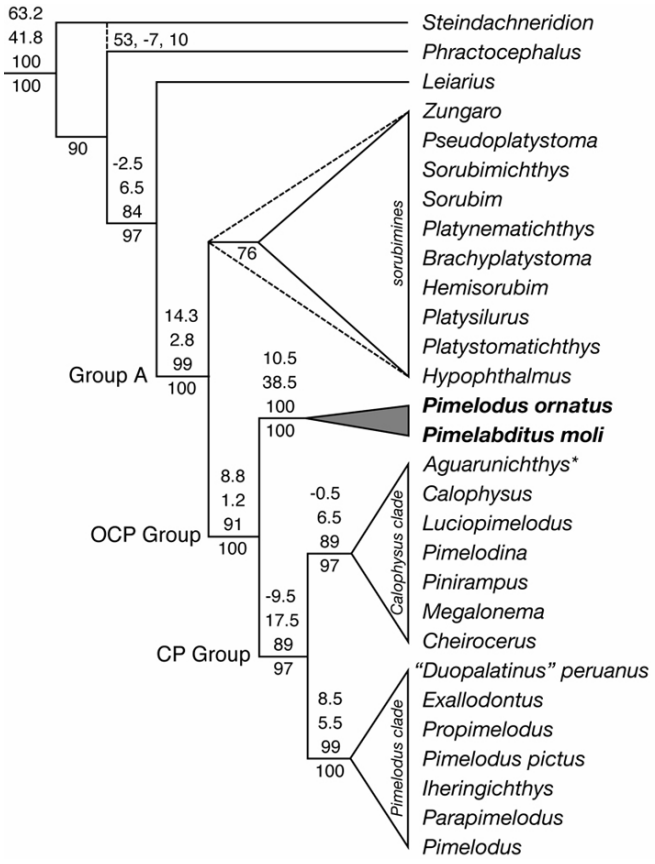

Figure 1. - Phylogenetic tree of monophyletic Pimelodidae illustrating the phylogenetic position of *Pimelabditus moli* among the major groups of the family; outgroup terminals representing Pseudopimelodidae and Heptapteridae are excluded from the figure. This tree is the Bootstrap majority rule consensus tree (consensus level = 50) from Maximum Likelihood and Maximum Parsimony analyses. Resulting topologies shown here are identical except as indicated by the dashed branches for the MP analysis in which *Steindachneridion* and *Phractocephalus* are sister genera, and the "sorubimines" clade collapses. Bootstrap proportions above 50 are shown on branches subtending selected nodes: bootstrap proportions for ML below the branches and for MP immediately above the branches (or to the right of dashed MP branch between *Steindachneridion* and *Phractocephalus*). Partitioned decay indices from MP are above the branches: uppermost the *rag* partition decay value, middle the mitochondrial partition decay value. The genus *Aguarunichthys*, for which we only have a part of the *mt-rnr1* sequence, is added to the tree within the *Calophysus* Group based on a separate molecular analysis and morphological synapomorphies (Stewart, 1986).

data, the partitioned decay indices (and the results of separate analyses) reveal conflicting signals between the *rag* (negative) and mitochondrial (positive) data partitions.

ML and MP analyses of the combined data support a much larger pimelodid lineage that largely corresponds to "Group A" of Lundberg *et al*. (1988). Here Group A contains the OCP Clade and, in ML, a weakly supported monophyletic array of genera labeled "sorubimines." In MP the sorubimines are not supported by a bootstrap proportion > 50%,

but all of the genera placed in it in ML remain in Group A. In ML, the three deepest phylogenetic splits in Pimelodidae produce the genera *Steindachneridion*, *Phractocephalus*, *Leiarius* (including *Perrunichthys*) in sequence below Group A. As noted above, MP differs in placing *Phractocephalus* sister to *Steindachneridion* but bootstrap support for this node is scant at 53%.

Phylogenetic results from separate data analyses

The RAxML analysis using only the *rag* gene data produces a tree of log likelihood -21285.98. The bootstrap consensus of the *rag*-data ML tree finds strong support for the *P. moli -P. ornatus* Clade and it placement in the OCP Clade. However, the tree differs from combined-data ML tree (Fig. 1) in placing the *P. moli -P. ornatus* Clade sister to the *Pimelodus* Group, rather than as the sister to a CP Clade. Bootstrap support for the *rag*-only ML node with *P. moli -P. ornatus* Clade + *Pimelodus* Group is lower (82) than the support for the CP node in both the combined-data ML (97) and the mitochondrial-only ML (99). The MP analysis using the *rag* gene data yielded 360 most parsimonious trees of 2,625 steps and a Consistency Index of 0.516 with uninformative characters excluded. The 50% bootstrap consensus of the MP trees, like ML for *rag*-only, finds the *P. moli -P. ornatus* Clade sister to the *Pimelodus* Group.

The RAxML analysis using the mitochondrial gene data gives a tree of log likelihood -37787.42. As noted above, the bootstrap consensus of the mitochondrial-only ML tree matches the combined-data ML tree (Fig. 1) in recovering the OCP Clade, and the CP Clade with *P. moli -P. ornatus* Clade sister to that. The MP analysis of the mitochondrial gene data yielded 9 most parsimonious trees of 7,229 steps and a Consistency Index of 0.255 with uninformative characters excluded. The bootstrap consensus of these nine MP trees is the least resolved topology of all results. In this, the mitochondrial data alone also support the *P. moli -P. ornatus* Clade and *Pimelodus* Group clade, but not the *Calophysus* Group, *CP* clade, OCP Clade, or Group A.

Morphology

As described previously by Parisi and Lundberg (2009), *P. moli* possesses the nested synapomorphic characters that successively diagnose the family Pimelodidae and the Group A clade within Pimelodidae (Lundberg *et al*., 1988; Nass, 1991). Further, *P. moli* was placed near, but not within, the *Calophysus-Pimelodus* Clade on the basis of its possession of two of the four synapomorphies marking that clade (Lundberg *et al*., 1991). That is, *P. moli* lacks a complete bony cleithral ring in the postemporo-supracleithrum-cleithrum joint, and has concave lateral margins of the ventral surface of the mesethmoid. We find that *Pimelodus ornatus*, like *P. moli*, has an incomplete cleithral ring in which the latero-ventral process of the supracleithrum and posterolateral extension of anterior limb of fourth transverse process fail to articulate, leaving a small gap.

Here we describe and compare anatomically complex structures of the otic-occipital region of the skull and associated pectoral girdle that provide additional evidence bearing on the phylogenetic position of *P. moli*.

The plesiomorphic condition of the otic-occipital region in pimelodids is shown by *Steindachneridion*, *Phractocephalus* and *Leiarius* (Fig. 2A), the phylogenetically deepest pimelodid genera. These taxa lack a pterotic-epioccipital fossa, the paroccipital fossa is shallow or planar, and the epioccipital bone is broad, roughly triangular in outline and gently projecting from the occipital wall over the posterior semicircular canal.

In contrast to the plesiomorphic condition, pimelodids of the OCP Clade have a prominent pair of paroccipital fossae (Fig. 2B-E). Each paroccipital fossa is a tall, wide and deeply excavated cavity flanking the midline structures of the supraoccipital, basioccipital and paired exoccipitals. The paroccipital fossa is bounded dorsally by the supraoccipital, laterally by the epioccipital (in particular its bony wall covering the posterior semicircular canal of the inner ear), and ventrally by the exoccipital.

In addition to the enlarged paroccipital fossae, pimelodids of the OCP Clade have paired pterotic-epioccipital fossae on the occipital wall lateral to the paroccipital fossae. In most OCP-Clade species the pterotic-epioccipital fossae (Fig. 2B) are small, shallow depressions between the pterotic and epioccipital bones, and placed ventrolateral to the paroccipital fossae. Also, as in the basal pimelodid genera, the epioccipital bone is wide, roughly triangular in outline and gently projecting from the occipital wall.

Pimelabditus moli and *P. ornatus* differ from CP-Clade pimelodids in having enlarged and strongly excavated pterotic-epioccipital fossae in a laterodorsal position on the occiput (Fig. 2C-E). Each pterotic-epioccipital has a large, ovoid aperture that leads to a deep chamber. The blind interior chamber of the pterotic-epioccipital fossa is dorsal to the otic capsule and walled by the pterotic, epioccipital, supraoccipital, extrascapula and upper limb of the posttemporo-supracleithrum. Furthermore in these two genera, each epioccipital is a narrowly compressed, vertical wall running from the supraoccipital to exoccipital and separating the paroccipital fossa from the pterotic-epioccipital fossa. The hypertrophied pterotic-epioccipital fossa and its associated complex occipital wall are an unambiguous synapomorphy of *P. moli* and *P. ornatus* that is not seen in other pimelodids.

DISCUSSION

The major clades of Pimelodidae recovered with high support in this molecular phylogenetic study of the com-

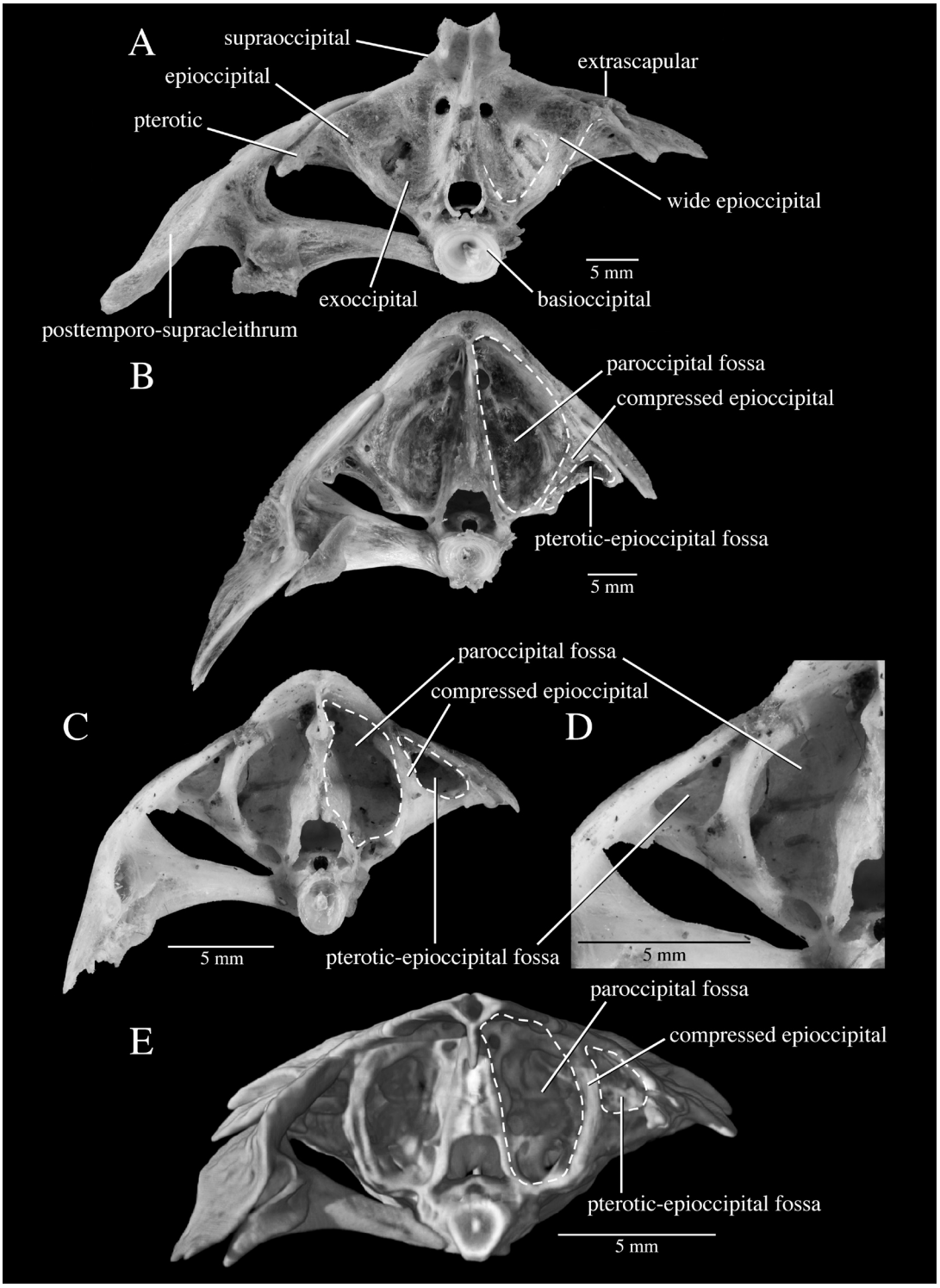

Figure 2. - Posterior views of the occipital region morphology of representative pimelodids to illustrate the deep pterotic-epioccipital fossa synapomorphy uniting *Pimelabditus moli* and *Pimelodus ornatus*. Dashed white lines show approximate limits of fossae and vertical ridge of epioccipital bone over posterior semicircular canal. **A**: *Leiarius marmoratus* ANSP 191359, dry skeleton showing plesiomorphic absences of pterotic-epioccipital and paroccipital fossae, and presence of wide epioccipital; **B**: *Pimelodus maculatus* MZUSP 78460, dry skeleton showing presence of deep, enlarged paroccipital fossa and relatively small, ventrolaterally placed pterotic-epioccipital fossa; **C**, **D**: *Pimelodus ornatus* ANSP 178452, dry skeleton showing deep, enlarged paroccipital fossa and enlarged, dorsolateraly-placed pterotic-epioccipital fossa and compressed epioccipital; **E**: *Pimelabditus moli* ANSP 188900, high resolution computed tomography. All scale bars = 5 mm.

bined *rag* and mitochondrial sequence data with *P. moli* added (Fig. 1) are almost identical to those of our previous and ongoing studies of Pimelodidae without *P. moli* (Hardman and Lundberg, 2006; Sullivan *et al*., 2006, pers. data; Lundberg *et al*., 2011). Morphological synapomorphies supporting monophyly of the family Pimelodidae and its major subgroups shown in figure 1 have been described (see references given in table I) and are generally in strong agreement with the molecular findings.

The novel results in the present work are the strong combined nuclear and mitochondrial gene signal and morphological evidence for the *P. moli -P. ornatus* Clade that is sister to the CP (*Calophysus-Pimelodus*) Clade, together forming the OCP Clade of Pimelodidae. Standard measures of molecular support for the *P. moli -P. ornatus* Clade are as high as they can be in the combined and partitioned analyses. The unique and anatomically complex synapomorphy of the pterotic-epioccipital fossa provides further support for the *P. moli -P. ornatus* Clade. The soft anatomy connected to the pterotic-epioccipital fossa and the biological role of this structure remains to be determined. In other aspects of their skeletal and external anatomy *P. ornatus* and *P. moli* are autapomorphically divergent or similar to features shared widely among pimelodids.

A significant taxonomic consequence of our results will be the removal of *Pimelodus ornatus* from the genus *Pimelodus*, the type species of which genus is *P. maculatus*. This taxonomic change has been long anticipated by Lundberg *et al*. (1991) and Lundberg and Parisi (2002), and will be published elsewhere. *Pimelodus ornatus* is also in need of species-level revision as it is likely a complex of three or more species (M. Rocha pers. comm.; pers. obs.).

Pimelabditus moli is known from only five specimens from four localities within the upper Maroni basin. Two additional small specimens are mentioned in the MNHN collection database, but no information on their origin is available. The species was collected in fast flowing waters in the main channel of the river in the immediate vicinity of waterfalls or rapids. In all places, the substrate was mainly boulders and stones, with gravels in the shallows, sand in the deeper, still water areas, and mud and decayed organic litter in the deepest holes. Exposed wet rocks were covered by river weed *Mourera fluviatilis* (Podostemaceae).

In Kumaru Konde Sula (type-locality, Tapanahony River, Suriname; the major tributary of the Maroni River), *P. moli* was collected at night using gillnets just upstream of the rapids. Depth ranged between 0 to 1.20 m, and water parameters were: temperature 30.1°C, pH 7.19, and conductivity 12 μS.cm^{-1}. In French Guiana, the only two specimens from Litany and Tampok Rivers were collected with ichthyocide by Wayana Amerindians. Coauthor Fisch-Muller had the opportunity to observe a large traditional fishing event that was organized by the people of Kayode village in the upper Tampok River, in a river reach that had not been fished for six years (Pagezy and Jégu, 2004). A fishing party of 169 Amerindians travelled upstream in 24 canoes for three days, ascending numerous rapids and falls up to Saut Pierkuru. Not less than 850 kg of liana (hali hali ichthyocide) was applied that resulted in a catch of nearly one ton of fish. In the catch that yielded more than a hundred of species, a single specimen of *Pimelabditus moli* was found. Despite the huge fishing effort, this new catfish species remained scarce. Surprisingly, the fact that three specimens were easily caught in Tapahony and Paloemeu rivers suggests that the species is more common in this drainage.

The riverine species associated with *P. moli* are mainly rheophilic fishes able to swim in turbulent flow, such as Serrasalmidae and Anostomidae, and species capable of maintaining their station on the substrate, such as Loricariidae, Characidiidae, Hemiodontidae and Parodontidae (Ouboter and Mol, 1993; Jégu *et al*., 2004). Endemism in the Maroni River basin may be estimated between seven to nine percents (20 of 305 species listed by Mol *et al*., 2012; 22 of 242 species by Meunier *et al*., 1998, for French Guiana only). Within the upstream fish community, three endemic catfishes were collected with *P. moli*: *Corydoras* aff. *breei*, *Hemiancistrus medians*, and Gen. nov. aff. *Parotocinclus* (sensu Le Bail *et al*., 2000) and two others were recorded from similar biotopes: *Hemiancistrus* aff. *braueri* and *Panaque* cf. *dentex*. Four of these endemic catfishes are also new taxa (see Fisch-Muller *et al*., 2012 and Mol *et al*., 2012), which is a large proportion but probably expected in such difficult-to-sample habitats (Vari and Ferraris, 2009).

This combined molecular and morphological phylogenetic study resolves the systematic position *P. moli* as the sister group of *P. ornatus*. The discovery of *Pimelabditus moli* has added a distinctive new catfish species to Pimelodidae and to the aquatic fauna of the eastern Guiana Shield.

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