Molecular Phylogenetics and Evolution 50 (2009) 345–363

Contents lists available at ScienceDirect

Molecular Phylogenetics and Evolution

journal homepage: www.elsevier.com/locate/ympev

RNF213, a new nuclear marker for acanthomorph phylogeny

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ARTICLE INFO

Article history:
Received 10 July 2008
Revised 11 November 2008
Accepted 15 November 2008
Available online 27 November 2008

Keywords:
Acanthomorpha
RNF213
Nuclear marker
Phylogeny
Reliability

ABSTRACT

We show that RNF213 is a nuclear gene suitable for investigating large scale acanthomorph teleosteans interrelationships. The gene recovers many clades already found by several independent studies of acanthomorph molecular phylogenetics and considered as reliable. Moreover, we performed phylogenetic analyses of three other independent nuclear markers, first separately and then of all possible combinations (Dettaï, A., Lecointre, G., 2004. In search of nothothenioid (Teleostei) relatives. Antarct. Sci. 16 (1), 71–85. URL http://dx.doi.org/10.1017/S0954102004) of the four genes. This was coupled with an assessment of the reliability of clades using the repetition index of Li and Lecointre (Li, B., Lecointre, G., 2008. Formalizing reliability in the taxonomic congruence approach. Article accepted by *Zoologica Scripta*. URL http://dx.doi.org/10.1111/j.1463-6409.2008.00361.x). This index was improved here to handle the incomplete taxonomic overlap among datasets. The results lead to the identification of new reliable clades within the 'acanthomorph bush'. Within a clade containing the Atherinomorpha, the Mugiloidei, the Plesiopidae, the Blennioidei, the Gobiesocoidei, the Cichlidae and the Pomacentridae, the Plesiopidae is the sister-group of the Mugiloidei. The Apogonidae are closely related to the Gobioidei. A clade named 'H' grouping a number of families close to stromateids and scombrids (Stromateidae, Scombridae, Trichiuridae, Chiasmodontidae, Nomeidae, Bramidae, Centrolophidae) is related to another clade named 'E' (Aulostomidae, Macrorhamphosidae, Dactylopteridae). The Sciaenidae is closely related to the Haemulidae. Within clade 'X' (Dettaï, A., Lecointre, G., 2004. In search of nothothenioid (Teleostei) relatives. Antarct. Sci. 16 (1), 71–85. URL http://dx.doi.org/10.1017/S0954102004), the Cottoidei, the Zoarcoidei, the Gasterosteidae, the Triglidae, the Scorpaenidae, the Sebastidae, the Synanceiidae, and the Congiopodidae form a clade. Within clade 'L' (Chen, W.-J., Bonillo, C., Lecointre, G., 2003. Repeatability of clades as a criterion of reliability: a case study for molecular phylogeny of Acanthomorpha (Teleostei) with larger number of taxa. Mol. Phylogenet. Evol. 26, 262–288; Dettaï, A., Lecointre, G., 2004. In search of nothothenioid (Teleostei) relatives. Antarct. Sci. 16 (1), 71–85. URL http://dx.doi.org/10.1017/S0954102004) grouping carangoids with flatfishes and other families (Centropomidae, Menidae, Sphyraenidae, Polynemidae, Echeneidae, Toxotidae, Xiphiidae), carangids are the stem-group of echeneids and coryphaenids, and sphyraenids are the sister-group to the Carangoidei. The Howellidae, the Epigonidae and the Lateolabracidae are closely related. We propose names for most of the clades repeatedly found in acanthomorph phylogenetic studies of various teams of the past decade.

1. Introduction

Acanthomorphs are a large group of more than 16,000 teleostean fish species. This monophyletic group is composed of some well supported clades but also of some poorly defined large assemblages like percomorphs, perciforms, scorpaeniforms. Most of these have been suspected not to be monophyletic for a long time (Stiassny et al., 2004). Morphology and comparative anatomy are difficult to use for phylogenetic purposes at such a large scale (see Stiassny and Moore, 1992, 1993). Even after the efforts to clarify acanthomorph interrelationships, synthesized by Johnson and Patterson (1993), many of the large clades retained later appeared strongly contradicted by molecular phylogenies (Chen et al., 2000, 2003, 2007; Dettaï and Lecointre, 2004, 2005, 2008, submitted for publication; Miya et al., 2001, 2003, 2005; Mabuchi et al., 2007; Kawahara et al., 2008; Smith and Wheeler, 2004, 2006; Smith and Craig, 2007). Paracanthopterygii, Acanthopterygii, Euacanthopterygii and Smegmamorpha, for instance, are all in this case. These large divisions had to be broken up because new contradicting groups were supported from independent molecular

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doi:10.1016/j.ympev.2008.11.013

studies. Percoids also are widely distributed among acanthomorphs, so at least the traditionally defined percomorphs, perciforms, scorpaeniforms and percoids can now be considered polyphyletic (see Dettaï and Lecointre, 2005, 2008, 2007).

Moreover, new groups emerged as a result of the analyses in a single matrix of a significant number of taxonomic components, often compared directly for the first time. The picture of large scale acanthomorph fish interrelationships changes rapidly, just like the mammalian tree changed as soon as enough genes were sequenced for all eutherian orders. However the acanthomorph revolution is far from being over. Large scale relationships are still poorly known: areas of irresolution remain and all 311 families (Nelson, 2006) have not yet been sampled. In spite of the recent spectacular advances, 'the bush at the top' (Nelson, 1989) persists. More acanthomorph families must be sampled, and in parallel, a higher number of phylogenetically efficient nuclear markers must be available (Li et al., 2007, 2008).

Reliability of phylogenetic findings is generally considered to be reached when several teams have found the same results independently from independent markers. This can be applied to the work of a single research team, by performing separate phylogenetic analyses of different independent molecular markers and checking for clade repetition across trees. Of course, it is necessary to base the study not only on mitochondrial markers, but also on carefully chosen, functionally and positionally independent nuclear markers. This comparative methodology was applied on acanthomorph by Chen et al. (2003), Dettaï and Lecointre (2004, 2005) and more recently by Miya et al. (2007) and Dettaï and Lecointre (submitted for publication). Studies using the partial rhodopsin retrogene (Chen et al., 2003), MLL (Dettaï and Lecointre, 2004, 2005) and IRBP (Dettaï and Lecointre, 2008) showed that these nuclear markers bear information relevant to the phylogeny of acanthomorphs. Other markers must be used more cautiously on this group and at this scale, like for instance 28S rDNA sequences (Chen et al., 2003) and TMO4C4 gene sequences (Smith and Wheeler, 2004). Therefore, there is still a need for additional, high phylogenetic quality markers. The availability of several teleost genomes opens new opportunities for the research of new markers, as also demonstrated by the study of Li et al., 2007, 2008. In the present study, we used the Ensembl Biomart mining tool and selected a few candidates markers. A promising locus, RNF213, was amplified for a representative sampling of teleost acanthomorphs, and compared to other large nuclear and mitochondrial datasets. Additionally, we performed combined and separate phylogenetic analyses with retro-rhodopsin, MLL and IRBP, and assessed the reliability of clades using the repetition index of Li and Lecointre (2008).

2. Materials and methods

2.1. Selection of the molecular markers

In the case of the interfamilial relationships of Acanthomorpha, the addition of new nuclear markers appears to be still necessary: the changes between the topologies and reliabilities between Chen et al. (2003) and Dettaï and Lecointre (2004, 2005, 2008) show that the inclusion of new markers increases the number of repeated clades even if the sampling is similar (Dettaï and Lecointre, 2005, 2008, submitted for publication).

In previous studies, we used protein-coding nuclear genes as well as mitochondrial (12S and 16S, Chen et al., 2003; Dettaï and Lecointre, 2004, 2005) and nuclear (28S, Chen et al., 2003) rDNA sequences. Alignment difficulties and low phylogenetic content of these rDNA genes with respect to the acanthomorph issue led us to abandon these markers and focus on carefully chosen nuclear protein-coding genes.

The Biomart mining tool of the Ensembl Portal (Hubbard et al., 2005) release 40 was used to get a list of protein-coding genes shared by *Tetraodon nigroviridis*, *Takifugu rubripes*, and *Danio rerio*, using *T. nigroviridis* as a query. Genes having unique best hits were retained, and checked for divergence and exon length through the Ensembl Portal on all the available teleost genomes. The sequence coding for RNF213 was again blasted (Altschul et al., 1997) on all available teleost genomes to check that it was a single copy marker in all. Last, it was blasted in the CoreNucleotide database of Genbank and all available sequences for acanthomorph species were recovered and used for primer design after alignment with Bioedit (Hall, 2001). The primers are listed in Table 1.

The previously published datasets for the retro-rhodopsin (simply noted 'Rhodopsin' afterwards), MLL and IRBP genes were completed with additional taxa (Table 2). To these, we added sequence data from the gene RNF213.

2.2. PCR and sequencing

DNA was extracted mostly from muscle samples stored in 70% ethanol, following the protocol of Winnepenninckx et al. (1993).

Table 1
Primers used in this study.

Primer	Sequence (5′ → 3′)	Forward/reverse	Source
Rh193	CNTATGAATAYCCTCAGTACTACC	Forward	Chen et al. (2003)
Rh667r	AYGAGCACTGCATGCCCT	Reverse	Chen et al. (2003)
Rh1039r	TGCTTGTTCATGCAGATGTAGA	Reverse	Chen et al. (2003)
Rh1073r	CCRCAGCACARCGTGGTGATCATG	Reverse	Chen et al. (2003)
MLL U1477	AGYCCAGCRGTCATCAAACC	Forward	Dettaï and Lecointre (2005)
MLL U1499	GTCAATCAGCAGTTCCAGC	Forward	Dettaï and Lecointre (2005)
MLL U1570	CCCYCAAAAKATCARTGCCAC	Forward	This study
MLL U1590	CRGGRGTGATNGACACCAGC	Forward	This study
MLL L2080	GTGAACTCMAYCAGTCCTCC	Reverse	This study
MLL 2105	ACCYTGCGTTGGGARGTGG	Reverse	This study
MLL L2158	ARAGTAGTGGGATCYAGRTACAT	Reverse	Dettaï and Lecointre (2005)
IRBP U104	ATAGTYNTGGACAANTACTGCTC	Forward	Dettaï and Lecointre (2008)
IRBP U110	TGGACAAYTACTGCTCRCCAGA	Forward	Dettaï and Lecointre (2008)
IRBP L936	CACGGAGGYTGAYNATCTTGAT	Reverse	Dettaï and Lecointre (2008)
IRBP L953	CNGGAAYYTGARCACGGAGG	Reverse	Dettaï and Lecointre (2008)
IRBP L1338	GTGRAAGGAGAYTTTGATCAGCTC	Reverse	Dettaï and Lecointre (2008)
C17 F3111	GCTGACTGGATTYAAAACCTT	Forward	This study
C17 F3128	CCTTTGTGGTGGAYTTYATGAT	Forward	This study
C17 F3150	WCTGATGGCNAARGACTTTGC	Forward	This study
C17 R4036	GGRATRGANCCNAGCTTTTCAT	Reverse	This study
C17 R4096	CCANACCAGAGGGATCATRCT	Reverse	This study
C17 R4111	AACTGTCCAAARTCCCACAC	Reverse	This study

Table 2
Sequences used in this study. Taxonomy follows Nelson, 2006, except for families, that are those present in Fishbase (Froese and Pauly, 2006). Sequences in boldface font are new sequences.

Order/suborder	Family	Genus/species	Rhosopsin	MLL	IRBP	RNF213
Argentiniformes						
Alepocephaloidei						
	Alepocephalidae	*Alepocephalus antipodianus* (Parrot, 1948)	**EU637933**	–	–	–
Stomiiformes						
Gonostomatoidei						
	Gonostomatidae	*Gonostoma bathyphilum* (Valliant, 1884)	AY141256	–	–	–
Aulopiformes						
Chlorophthalmoidei						
	Ipnopidae	*Bathypterois dubius* Vallian, 1888	**AY141257**	AY362219	DQ168042	–
Myctophiformes						
	Myctophidae	*Electrona antarctica* (Günther, 1878)	AY141258	AY36220	–	–
Lampriformes						
	Lampridae	*Lampris immaculatus* Gilchrist, 1904	AY141259	–	DQ168077	–
	Trachipteridae	*Trachipterus arcticus* (Brünnich, 1788)	–	–	**EU638158**	–
	Regalecidae	*Regalecus glesene* Ascanius, 1772	AY368328	AY362266	DQ168109	**EU638252**
Polymixiiformes						
	Polymixiidae	*Polymixia nibilis* Lowe, 1838	AY368320	AY362208	DQ168104	–
Percopsiformes						
	Apherdoderidae	*Aphredoderus sayanus* (Gilliams, 1824)	–	–	DQ168038	–
Gadiformes						
	Muraenolepididae	*Muraenolepsis marmorata* Günther, 1880	–	**EU638073**	–	–
	Macrouridae	*Coryphaeniides rupestris* Gunnerus, 1765	AY368319	**EU638041**	–	–
	Macrouridae	*Trachyrincus murrayi* Günther, 1887	AY368318	**AY362289**	DQ168124	**EU638270**
	Moridae	*Mora moro* (Risso, 1810)	AY368322	**EU638071**	DQ168089	**EU638227**
	Merlucciidae	*Merluccius merluccis* (L., 1758)	–	**EU638068**	–	–
	Phycidae	*Phcis physics* (L., 1766)	**EU637994**	–	–	–
	Lotidae	*Enchelyopus cimbrius* (L., 1766)4	**EU637958**	–	–	–
	Lotidae	*Gaidropsarus* (Hector, 1874)	–	**EU638051**	–	–
	Lotidae	*Gaidropsarus* sp.	**EU637961**	–	–	–
	Lotidae	*Gaidropsarus vulgaris* (Cloquet, 1824)	–	–	DQ168067	–
	Gadidae	*Gadus morhua* L., 1758	AF137211	**EU638050**	DQ168066	–
	Gadidae	*Merlangius merlangus* (L., 1758)	AY141260	–	–	–
Ophidiiformes						
Ophidioidei						
	Carapidae	*Encheliophis boroborensis* (Kaup, 1856)	–	–	–	**EU638179**
	Carapidea	*Echiodon cryomargarites* Markle, Williams & Olney,1983	**EU637956**	–	–	–
	Ophidiidae	*Lamprogrammus scherbachevi* Cohen & Rohr, 1993	**EU637969**	**EU638058**	**EU638130**	–
Bythitoidei						
	Bythitidae	*Cataetyx laticeps* Koefoed, 1927	**EU637947**	**EU638035**	–	–
Batrachoidiformes						
	Batrachoididae	*Halobatrachus didactylus* (Bloch Schneider, 1801)	AY368323	AY362246	DQ168069	**EU638205**
Lophiiformes						
Lophioidei						
	Lophiidae	*Lophius budegassa* Spinola, 1807	–	–	–	**EU638217**
	Lophiidae	*Lophius piscatorius* L., 1758	AY368325	AY362274	–	–
Antennarioidei						
	Antennariidae	*Antennarius striatus* (Shaw, 1794)	AY368324	AY362215	DQ168037	–
Ogcocephaloidei						
	Himantolophidae	*Himantolophus groenlandicus* Reinhardt,1837	**EU637965**	**EU638055**	**EU638125**	–
	Ceratiidae	*Ceratias holboelli* Krøyer, 1845	AY141263	AY362270	DQ168049	**EU638181**
Mugiliformes						
	Mugilidae	Liza sp.	AY141266	AY362248	DQ168082	–
Atheriniformes						
	Atherinopsidae	*Menidia menidia* (L., 1766)	**EU637977**	**EU638067**	**EU638137**	–
	Bedotiidae	*Bedotia geayi* Pellegrin, 1907	AY141267	AY362271	DQ168043	–
Beloniformes						
	Adrianichthyidae	*Oryzias latipes* (Temminck	Schlegel, 1946)	–	– DQ168094	Ensembl
	Exocoetidae	*Cheilopogon heterurus* (Rafinesque, 1810)	**EU637950**	**EU638039**	**EU638113**	**EU638184**
	Belonidae	*Belone belone* (L., 1761)	AY141268	AY362273	DQ168044	–
Cyprinodontiformes						
	Anablepidae	*Anableps anableps* (L., 1758)	**EU637935**	–	–	–
	Poeciliidae	*Poecilia reticulata* Peters, 1859	Y11147	AY362203	DQ168102	**EU638243**
Stephanoberyciformes						
	Rondeletiidae	*Rondeletia* sp.	AY368327	**EU638087**	DQ168110	–
	Barbourisiidae	*Barbourisia rufa* Parr, 1945	AY368333	AY362264	DQ168041	–

(*continued on next page*)

Table 2 (*continued*)

Order/suborder	Family	Genus/species	Rhosopsin	MLL	IRBP	RNF213
Beryciformes						
Trachichthyoidei						
	Anomalopidae	*Photoblepharon palpebratum* (Boddaert, 1781)	**EU637993**	AY362268	DQ168101	**EU638242**
	Diretmidae	*Diretmoides* sp.	–	AY362205	DQ168060	–
	Trachichthyidae	*Hoplostethus atlanticus* Collett, 1889	–	–	**EU638127**	**EU638207**
	Trachichthyidae	*Hoplostethus mediterraneus* Cuvier, 1829	AY141264	AY362267	–	–
Berycoidei						
	Berycidae	*Beryx splendens* Lowe, 1834	AY141265	AY362238	DQ168045	**EU638174**
Holocentroidei						
	Holocentridae	*Myripristis botche* Cuvier, 1929	–	AY362265	DQ168091	–
	Holocentridae	*Myripristis* sp.	**EU637983**	–	–	**EU638230**
Zeiformes						
	Oreosomatidae	*Neocyttus helgae* (Holt Byrne, 1908)	AY141261	**AY362288**	–	–
	Grammicolepididae	*Grammicolepis brachiusculus* Poey, 1873	**EU637964**	**EU638054**	**EU638124**	–
	Zeidae	*Zenopsis conchifera* (Lowe, 1852)	AY368314	AY362286	DQ168127	**EU638279**
	Zeidae	*Zeus faber* L., 1758	**EU638023**	**AY362287**	DQ168128	–
Gasterosteiformes						
Gasterosteoidei						
	Gasterosteidae	*Gasterosteus aculeatus* L., 1758	**EU637962**	**EU638052**	Ensembl	Ensembl
	Gasterosteidae	*Spinachia spinachia* (L., 1758)	AY141281	AY362261	–	**EU638264**
	Indostomidae	*Indostomus paradoxus* Prashad & Mukerji, 1929	**EU637967**	**EU638057**	–	**EU638209**
Syngnathoidei						
	Syngnathidae	*Hippocampus guttulatus* Cuvier, 1829	AY368330	AY362216	**EU638126**	–
	Syngnathidae	*Nerophis lumbriciformis* (Jenyns, 1835)	**EU637987**	–	**EU638143**	**EU638232**
	Syngnathidae	*Nerophis ophidion* (L., 1758)	–	–	DQ168071	–
	Syngnathidae	*Syngnathus typhle* L., 1758	AY368326	AY362211	DQ168120	–
	Fistulariidae	*Fistularia petimba* Lacèpède, 1803	AY141324	–	–	**EU638202**
	Aulostomidae	*Aulostomus chinensis* (L., 1766)	AY141279	AY362226	DQ168040	–
	Centriscidae	*Aeoliscus strigatus* (Günther, 1861)	**EU637931**	–	**EU638100**	–
	Centriscidae	*Macroramphosus scolopax* (L., 1758)	AY141280	AY362206	DQ168083	–
Symbranchiformes						
Symbranchoidei						
	Symbranchidae	*Monopterus albus* (Zuiew, 1793)	AY141276	AY362252	DQ168088	**EU638226**
Mastacembeloidei						
	Mastacembelidae	*Mastacembelus erythrotaenia* Bleeker, 1850	**AY141275**	**AY362249**	**DQ168084**	–
Scorpaeniformes						
Dactylopteroidei						
	Dactylopteridae	*Dactylopterus volitans* (L., 1758)	AY141282	AY362243	DQ168059	–
Scorpaenoidei						
	Sebastidae	*Sebastes* sp.	–	–	–	**EU638258**
	Scorpaenidae	*Pontinus longispinis* Goode Bean, 1896	**EU637996**	**EU638081**	**EU638146**	**EU638247**
	Scorpaenidae	*Scorpaena onaria* Jordan Snyder, 1900	AY141288	AY362236	DQ168114	**EU638257**
	Synanceiidae	*Synanceia verrucosa* Bloc Schneider, 1801	EU638011	EU638093	**EU638156**	**EU638267**
	Congiopodidae	*Zanclorhynchus spinifer* Günther, 1880	**EU638021**	–	**EU638165**	**EU638278**
Platycephaloidei						
	Triglidae	*Chelidonichthys lucernus* (L., 1758)	AY141287	AY362284	DQ168053	**EU638186**
Cottoidei						
	Cottidae	*Taurulus bubalis* Euphrasen, 1786)	U97275	AY362217	DQ168121	–
	Agonidae	*Agonopsis chiloensis* (Jenyns, 1840)	**EU637932**	**EU638025**	**EU638101**	**EU638167**
	Agonidae	*Xeneretmus latifrons* (Gilbert, 1890)	**EU638018**	**EU638097**	**EU638162**	–
	Psychrolutidae	*Cottunculus thomsonii* (Günther, 1882)	AY368315	AY362260	–	–
	Cyclopteridae	*Cyclopterus lumpus* L., 1758	AY368316	**AY362218**	**EU638116**	–
	Liparidae	*Liparis fabricii* Krøyer, 1847	AY368317	AY362235	DQ168081	–
Perciformes						
Percoidei						
	Centropomidae	*Centropomus undecimalis* (Bloch, 1792)	–	–	–	**EU638180**
	Lateolabracidae	*Lateolabrax japonicus* (Cuvier, 1828)	AY141293	AY362253	DQ168078	**EU638213**
	Latidae	*Lates calcarifer* (Bloch, 1970)	**EU637970**	**EU638059**	DQ168075	**EU638214**
	Latidae	*Lates niloticus* (L., 1758)	**EU637971**	–	–	–
	Moronidae	*Dicentrarchus labrax* (L., 1758)	–	–	**EU638119**	**EU638195**
	Moronidae	*Morone saxatilis* (Walbaum, 1792)	**EU637981**	**EU638072**	**EU638140**	**EU638228**
	Percichthyidae	*Howella brodiei* (Ogilby, 1899)	**EU637966**	**EU638056**	**EU638128**	**EU638208**
	Serranidae	*Acanthistius brasilianus* (Cuvier, 1828)	–	**EU638024**	–	–
	Serranidae	*Cephalopholis urodeta* (Forster, 1801)	–	**EU638036**	–	–
	Serranidae	*Dermatolepis dermatolepis* (Boulenger, 1895)	–	**EU638045**	–	–
	Serranidae	*Epinephelus aeneus* (Geoffroy Saint-Hilaire, 1817)	AY141291	**EU638049**	AY362227	**EU638201**
	Serranidae	*Odontanthias chrysostictus* (Günther, 1872)	**AY141290**	**AY362209**	**DQ168073**	**EU638206**
	Serranidae	*Liopropoma fasciatum* Bussing, 1980	–	**EU638062**	–	–
	Serranidae	*Niphon spinosus* Cuvier, 1828	**EU637934**	–	–	–
	Serranidae	*Plectropomus leopardus* (Lacèpède, 1802)	–	**EU638078**	–	–
	Serranidae	*Pogonoperca punctata* (Valenciennes, 1830)	AY141292	AY362256	DQ168103	**EU638244**
	Serranidae	*Pseudanthias squamipinnis* (Peters, 1855)	–	**EU638083**	–	–

Table 2 (*continued*)

Order/suborder	Family	Genus/species	Rhosopsin	MLL	IRBP	RNF213
	Serranidae	*Rypticus saponaceus* (Bloch Schneider, 1801)	AY368329	**AY362257**	**DQ168111**	**EU638253**
	Serranidae	*Serranus accraensis* (Norman, 1931)	AY141289	AY362202	DQ168115	**EU638260**
	Callanthiidae	*Callanthias ruber* (Rafinesque, 1810)	**EU637945**	**EU638034 EU638110**	–	
	Plesiopidae	*Assessor flavissimus* Allen Kuiter, 1976	**EU637944**	**EU638032**	**EU638109**	**EU638173**
	Centrarchidae	*Lepomis gibbosus* (L., 1758)	AY742571	**EU638061**	**EU638132**	**EU638216**
	Percidae	*Gymnocephalus cernuus* (L., 1758)	AY141296	AY362278	DQ168068	–
	Percidae	*Perca fluviatilis* L., 1758	AY141295	AY362279	DQ168099	**EU638240**
	Priacanthidae	*Priacanthus arenatus Cuvier*, 1829	**EU637997**	**EU638082**	**EU638147**	–
	Epigonidae	*Epigonus telescopus* (Risso, 1810)	**EU637959**	**EU638048**	**EU638122**	**EU638200**
	Apogonidae	*Apogon fasciatus* (White, 1970)	**EU637940**	–	–	**EU638171**
	Apogonidae	*Sphaeramia nematoptera* (Bleeker, 1856)	**EU638010**	**EU638091**	**EU638154**	–
	Malacanthidae	*Lopholatilus chamaeleonticeps* Goode & Bean, 1879	**EU637973**	**EU638063**	**EU638133**	**EU638218**
	Sillaginidae	*Sillago sihama* (Forsskål, 1775)	**EU638008**	–	–	**EU638262**
	Coryphaenidae	*Coryphaena equiselis* L., 1758	**EU637951**	**EU638040**	**EU638114**	**EU638189**
	Coryphaenidae	*Coryphaena hippurus* L., 1758	–	–	DQ168056	–
	Echeneidae	*Echeneis naucrates* L., 1758	AY141315	AY362245	DQ168062	**EU638197**
	Carangidae	*Chloroscombrus chrysurus* (L., 1766)	AY141313	AY362223	DQ168054	**EU638187**
	Carangidae	*Gnathanodon speciosus* (Forsskål, 1755)	**EU637963**	**EU638053**	**EU638123**	**EU638204**
	Carangidae	*Selene dorsalis* (Gill, 1863)	**EU638006**	**EU638089**	**EU638153**	**EU638259**
	Carangidae	*Trachinotus ovatus* (L., 1758)	AY141314	AY362263	DQ168120	–
	Carangidae	*Trachurus trachurus* (L., 1758)	**EU638013**	–	**EU638159**	**EU638269**
	Menidae	*Mene maculata* (Bloch & Schneider, 1801)	**AY141316**	**AY362250**	DQ168085	**EU638221**
	Leiognathidae	*Leiognathus fasciatus* (Lacépède, 1803)	**EU637972**	**EU638060**	**EU638131**	–
	Bramidae	*Pterycombus brama Fries*, 1837	**EU638001**	**EU638086**	**EU638149**	**EU638251**
	Lutjanidae	*Apsilus fuscus* Valenciennes, 1830				
	Lutjanidae	*Lutjanus sebae* (Cuvier, 1816)	**EU637974**	**EU638064**	**EU638134**	**EU638219**
	Caesionidae	*Pterocaesio digramma* (Bleeker, 1864)	**EU638000**	**EU638085**	**EU638148**	**EU638250**
	Datnioididae	*Datnioides polota* (Hamilton, 1822)	**EU637954**	**EU638044**	**EU638118**	**EU638194**
	Haemulidae	*Pomadasys perotaei* (Cuvier, 1830)	–	AY362230	DQ168105	**EU638246**
	Sparidae	*Spondyliosoma cantharus* (L., 1758)	–	**EU638092**	**EU638155**	**EU638265**
	Sciaenidae	*Argyrosomus regius* (Asso, 1801)	**EU637942**	**EU638030**	**EU638107**	**EU638172**
	Sciaenidae	*Johnius* sp. Bloch, 1793	–	–	**EU638129**	–
	Sciaenidae	*Micropogonias furnieri* (Desmarest, 1823)	**EU637979**	–	–	–
	Sciaenidae	*Micropogonias* sp.	–	–	–	**EU638224**
	Sciaenidae	*Sciaena* sp.	**EU638004**	–	–	–
	Polynemidae	*Pentanemus quinquarius* (L., 1758)	AY141317	AY362272	DQ168098	**EU638239**
	Mullidae	*Mullus surmuletus* L., 1758	**EU637982**	AY362231	DQ168090	**EU638229**
	Toxotidae	*Toxotes* sp.	**EU638012**	**EU638094**	**EU638157**	–
	Monodactylidae	*Monodactylus* sp. Lacépède, 1801	**EU637980**	**EU638070**	**EU638139**	–
	Kyphosidae	*Microcanthus strigatus* (Cuvier, 1831)	**EU637978**	**EU638069**	**EU638138**	**EU638222**
	Chaetodontidae	*Chaetodon semilarvatus* Cuvier, 1831	AY368312	AY362240	DQ168050	–
	Drepaneidae	*Drepane africana* Osório, 1892	AY141321	AY362244	DQ168061	**EU638196**
	Pomacanthidae	*Holacanthus ciliaris* (L., 1758)	AY141322	AY362214	DQ168072	–
	Pomacanthidae	*Pomacanthus maculosus* (Forsskål, 1775)	**EU637995**	**EU638079**	**EU638145**	**EU638245**
	Terapontidae	*Pelates quadrilineatus* (Bloch, 1790)	**EU637991**	–	–	–
	Cheilodactylidae	*Nemadactylus monodactylus* (Carmichael, 1819)	**EU637985**	**EU638075**	**EU638142**	**EU638231**
	Aplodactylidae	*Aplodactylus punctatus* Valenciennes, 1832	**EU637939**	–	–	–
	Cepolidae	*Cepola macrophthalma* (L., 1758)	**EU637948**	**EU638037**	**EU638111**	–
Elassomatoidei						
	Elassomatidae	*Elassoma zonatum* Jordan, 1877	**EU637957**	–	DQ168063	–
Labroidei						
	Cichlidae	*Haplochromis nubilus* (Boulenger, 1906)	–	–	DQ168070	–
	Cichlidae	*Haplochromis* sp.	AB084933	–	–	–
	Pomacentridae	*Dascyllus trimaculatus* (Rüppenl, 1829)	**EU637953**	**EU638043**	**EU638117**	**EU638193**
	Labridae	*Labrus bergylta* Ascanius, 1767	AY141318	AY362222	DQ168075	**EU638211**
	Labridae	*Xyrichtys novacula* (L., 1758)	**EU638020**	–	**EU638164**	**EU638277**
	Scaridae	*Scarus hoefleri* (Steindachner, 1881)	AY141319	AY362212	DQ168112	**EU638254**
Zoarcoidei						
	Zoarcidae	*Austrolycus depressiceps* Regan, 1913	AY141297	–	–	–
	Zoarcidae	*Lycodapus antarcticus* Tomo, 1982	**EU637976**	**EU638066**	**EU638136**	–
	Pholidae	*Pholis gunnellus* (L., 1758)	AY141298	AY362285	DQ168100	**EU638241**
	Anarhichadidae	*Anarhichas lupus* L., 1758	**EU637936**	**EU638026**	**EU638103**	**EU638169**
Notothenioidei						
	Nototheniidae	*Notothenia coriiceps* Richardson, 1844	AY141302	AY362282	DQ168093	–
	Nototheniidae	*Trematomus bernachii* Boulenger, 1902	**EU638014**	–	**EU638160**	**EU638271**
	Bovichtidae	*Bovichtus variegatus* Richardson, 1846	**AY141299**	AY362283	DQ168046	**EU638176**
	Bovichtidae	*Cottoperca trigliodes* (Forster, 1801)	AY141300	–	–	–
	Bovichtidae	*Pseudaphritis urvillii* (Valenciennes, 1832)	AY141301	–	–	–
	Eleginopsidae	*Eleginops maclovinus* (Cuvier, 1830)	AY141303	**EU638047**	**EU638121**	**EU638199**
	Channichthyidae	*Chionodraco hamatus* (Lönnberg, 1905)	AY362280	–	–	
	Channichthyidae	*Neopagetopsis ionah* Nybelin, 1947	**EU637986**	AY362281	DQ16802	–
	Channichthyidae	*Pagetopsis macropterus* (Boulenger, 1907)	**EU637990**	**EU638076**	**EU638144**	**EU638235**
Trachinoidei						
	Chiasmodontidae	*Kali macrura* (Parr, 1933)	AY141308	AY362224	DQ168074	**EU638210**

(*continued on next page*)

Table 2 (*continued*)

Order/suborder	Family	Genus/species	Rhosopsin	MLL	IRBP	RNF213
	Champsodontidae	*Champsodon snyderi* Franz, 1910	**EU637949**	**EU638038**	–	**EU638182**
	Pinguipedidae	*Parapercis clathrata* Ogilby, 1910	–	**EU638077**	–	**EU638238**
	Pinguipedidae	*Pinguipes chilensis* Valenciennes, 1833	**EU637989**	–	–	**EU638234**
	Cheimarrichthyidae	*Cheimarrichthys fosteri* Haast, 1874	**AY141307**	AY362229	DQ168052	**EU638185**
	Trachinidae	*Echiichthys vipera* (Cuvier, 1829)	**EU637955**	**EU638046**	**EU638120**	**EU638198**
	Trachinidae	*Trachinus draco* L., 1758	AY141304	AY362277	DQ168123	**EU638268**
	Ammodytidae	*Ammodytes tobianus* L., 1758	AY141306	AY362234	**EU638102**	**EU638168**
	Uranoscopidae	*Uranoscopus albesca* Regan, 1915	AY141305	AY362239	**DQ168126**	**EU638275**
Blennioidei						
	Tripterygiidae	*Forsterygion lapillum* Hardy, 1989	AY141272	AY362276	DQ168065	**EU638203**
	Tripterygiidae	*Tripterygion delaisi* Cadenat & Blache, 1970	**EU638016**	–	–	**EU638274**
	Blenniidae	*Parablennius gattorugine* (L., 1758)	AY141271	AY362255	DQ168097	**EU638237**
	Blenniidae	*Salaria pavo* (Risso, 1810)	Y18674	–	–	–
Gobiesocoidei						
	Gobiesocidae	*Apletodon dentatus* (Facciolà, 1887)	AY141274	AY362213	DQ168039	–
	Gobiesocidae	*Aspasma minima* (Döderlein, 1887)	**EU637943**	**EU638031**	**EU638108**	–
	Gobiesocidae	*Lepadogaster lepadogaster* (Bonnaterre, 1788)	AY141273	AY362247	DQ168080	**EU638215**
Callionymoidei						
	Callionymidae	*Callionymus lyra* L., 1758	AY141270	AY362225	DQ168047	**EU638177**
	Callionymidae	*Callionymus schaapii* Bleeker, 1852	**EU637946**	–	–	–
Gobioidei						
	Eleotridae	*Ophiocara porocephala* (Valenciennes, 1837)	**EU637988**	–	–	–
	Gobiidae	*Favonigobius reichei* (Bleeker, 1853)	**EU637960**	–	–	–
	Gobiidae	*Periophthalmus barbarus* (L., 1766)	**EU637992**	–	–	–
	Gobiidae	*Pomatoschistus minutus* (Pallas, 1770)	X62405	–	–	–
	Gobiidae	*Pomatoschistus* sp. Gill, 1863	–	**EU638080**	DQ168106	–
	Gobiidae	*Valenciennea strigata* (Broussonet, 1782)	**EU638017**	–	–	–
	Microdesmidae	*Ptereleotris zebra* (Fowler, 1938)	**EU637999**	**EU638084**	–	–
Acanthuroidei						
	Scatophagidae	*Selenotoca multifasciata* (Richardson, 1846)	**EU638002**	**EU638088**	**EU638150**	–
	Siganidae	*Siganus vulpinus* (Schlegel & Müller, 1845)	**EU638007**	**EU638090**	DQ168116	**EU638261**
	Luvaridae	*Luvarus imperialis* Rafinesque, 1810	**EU637975**	**EU638065**	**EU638135**	**EU638220**
	Acanthuridae	*Ctenochaetus* sp.	–	–	–	**EU638190**
	Acanthuridae	*Ctenochaetus striatus* (Quoy & Gaimard, 1825)	AY141320	AY362242	DQ168057	–
	Acanthuridae	*Naso lituratus* (Forster, 1801)	**EU637984**	**EU638074**	**EU638141**	–
Scombroidei						
	Sphyraenidae	*Sphyraena sphyraena* (L., 1758)	AY141312	AY362254	DQ168118	**EU638263**
	Trichiuridae	*Aphanopus carbo* Lowe, 1839	**EU637938**	**EU638028**	**EU638105**	**EU638170**
	Scombridae	*Scomber japonicus* Houttuyn, 1782	AY141311	AY362237	DQ168113	–
	Xiphiidae	*Xiphias gladius* L., 1758	**EU638019**	**EU638098**	**EU638163**	**EU638276**
Stromateoidei						
	Centrolophidae	*Psenopsis anomala* (Temminck & Schlegel, 1844)	AY141310	AY362269	DQ168107	**EU638248**
	Centrolophidae	*Schedophilus medusophagus* (Cocco, 1839)	**EU638003**	**EU660040**	**EU638151**	**EU638255**
	Nomeidae	*Cubiceps gracilis* (Lowe, 1843)	**EU637952**	**EU638042**	**EU638115**	**EU638192**
	Stromateidae	*Pampus argenteus* (Euphrasen, 1788)	AY141309	AY362220	DQ168096	**EU638236**
Anabantoidei						
	Anabantidae	*Ctenopoma* sp.	AY141278	AY362210	DQ168058	**EU638191**
Channoidei						
	Channidae	*Channa* sp.	–	–	–	**EU638183**
	Channidae	*Channa striata* (Bloch, 1793)	AY141277	AY362241	DQ168051	–
Caproidei						
	Caproidae	*Antigonia capros* Lowe, 1843	**EU637937**	**EU638027**	**EU638104**	–
	Caproidae	*Capros aper* (L., 1758)	AY141262	AY362233	DQ168048	**EU638178**
Pleuronectiformes						
Psettodoidei						
	Psettodidae	*Psettodes belcheri* Bennett, 1831	EU637998	AY362259	DQ168108	**EU638249**
Pleuronectoidei						
	Citharidae	*Citharus linguatula* (L., 1758)	AY141323	AY362232	DQ168055	**EU638188**
	Paralichthyidae	*Syacium micrurum* Ranzani, 1842	AY368334	AY362262	DQ168119	**EU638266**
	Scophthalmidae	*Scophthalmus rhombus* (L., 1758)	**EU638005**	–	**EU638152**	**EU638256**
	Scophthalmidae	*Zeugopterus punctatus* (Bloch, 1787)	**EU638022**	**EU638099**	**EU638166**	**EU638280**
	Bothidae	*Arnoglossus imperialis* (Rafinesque, 1810)	AY141283	AY362228	–	–
	Bothidae	*Bothus podas* (Delaroche, 1809)	AY368313	**EU638033**	–	**EU638175**
	Achiridae	*Trinectes maculatus* (Bloch & Schneider, 1801)	**EU638015**	**EU638096**	**EU638161**	**EU638273**
	Soleidae	*Microchirus frechkopi* Chabanaud, 1952	–	–	–	**EU638223**
	Soleidae	*Microchirus variegatus* (Donovan, 1808)	AY141284	AY362275	DQ168086	–
	Soleidae	*Solea solea* (L., 1758)	**EU638009**	–	**DQ168117**	–
Tetraodontiformes						
Triacanthodoidei						
	Triacanthodidae	*Triacanthodes anomalus* (Temminck & Schlegel, 1850)	–	**EU638095**	–	**EU638272**
	Triacanthodidae	*Triacanthodes* sp.	AY368331	–	DQ168125	–

Table 2 (*continued*)

Order/suborder	Family	Genus/species	Rhosopsin	MLL	IRBP	RNF213
Balistoidei						
	Balistidae	*Balistes* sp.	AF137212	–	–	–
	Ostraciidae	*Ostracion cubicus* L., 1758	–	–	–	**EU638233**
	Ostraciidae	*Ostracion* sp.	AF137213	AY362207	DQ168095	–
Tetraodontoidei						
	Tetraodontidae	*Lagocephalus laevigatus* (L., 1766)	–	AY362221	DQ168076	–
	Tetraodontidae	*Lagocephalus lagocephalus* (L., 1758)	**EU637968**	–	–	**EU638212**
	Tetraodontidae	*Takifugu rubripes* (Temminck & Schlegel, 1850)	–	Ensembl	Ensembl	Ensembl
	Tetraodontidae	*Tetraodon nigroviridis* Marion de Procé, 1822	Ensembl	Ensembl	Ensembl	Ensembl
	Molidae	*Mola mola* (L., 1758)	AF137215	AY362251	DQ168087	**EU638225**

The primers published in Chen et al. (2003) for Rhodopsin, in Dettaï and Lecointre (2005) for MLL and in Dettaï and Lecointre (2008) for IRBP were used, but 4 new primers were designed for MLL in order to obtain more gadiform sequences, and 6 new primers were used to amplify the new RNF213 marker (Table 1). Most RNF213 sequences could be obtained with primers C17 F3111 and C17 R4111. Various PCR conditions were used, depending on the primers and the DNA sample. Three different polymerases were used for the PCRs: Taq Appligen, QbioTaq and Taq Qiagen. PCRs began with a denaturation phase at 94 °C for 2–5 min and ended with a final elongation phase at 72 °C (or 68 °C for the longest PCRs using Taq Qiagen) for 4–7 min. Cycles began with a denaturation phase at 94 °C for 20–40 s, followed by an annealing phase at temperatures ranging from 47 to 60 °C and during from 25 to 45 s. The annealing phase was followed by an elongation phase at 72 °C (or 68 °C for the longest PCRs using Taq Qiagen) for 35 s to 2 min. The number of cycles ranged from 35 to 60. Purification and sequencing of the PCRs were performed at the Genoscope (http://www.genoscope.cns.fr/). The same primers were used for PCR and sequencing. Sequences were checked individually using Sequencher (Gene Codes Corporation) and aligned by hand using Se-Al (Rambaut, 2002). Indels were grouped by 3 so as to fit the coding frame, and adjusted according to the translation in amino acid sequences.

Characteristics of the aligned markers are given in Table 3.

Preliminary distance trees were done using PAUP* (Swofford, 2002) to check for contaminations. Accession numbers are given in Table 2.

2.3. Analysis strategy

When a clade contradicts the previously supported phylogenetic hypotheses, it is necessary to check whether this is due to an artifact. Those can be detected by using different taxonomic samplings, tree reconstruction methods, or, more reliably, by comparing the topology to the one inferred from an independent dataset. This is the primary reason to perform separate analyses in molecular phylogenetics. If selective pressures characterizing mutational space at each position are relatively homogeneous within genes but heterogeneous among genes, the fact that a given clade is recurrently recovered from independent markers is a strong indication of its reliability (Nelson, 1979; Chen et al., 2003; Dettaï and Lecointre, 2004, 2005).

Indeed, finding a clade twice independently just by chance is very improbable (Page and Holmes, 1998), and the probability of obtaining exactly the same tree reconstruction artifact from independent genes is also low, although sometimes the notorious long branch attraction artifact can occur with several markers when higher mutation rates affect large parts of the genome of several of the included species. Separate analyses tend to be more subject to stochastic errors (because of the shorter length of the analyzed sequences), but also prone to marker-specific biases. The recovery of a clade in separate analyses of several independent markers in spite of these problems is therefore a strong indication of the reliability of the clade. This led to the definition of a repetition index based on the number of occurrences of a clade across independent analyses (Li and Lecointre, 2008). This can also be used to detect instances where the markers reflect distinct and incompatible histories. Repetition across trees based on independent data is a better indicator than bootstrap proportions extracted from a crude 'total evidence' (for a review of the origins of that term, see Rieppel, 2004; Lecointre and Deleporte, 2005), because tree reconstruction artifacts can lead to clades with high robustness (Philippe and Douzery, 1994). Additionally, a positively misleading signal from a single gene can impose the topology of some parts of the tree inferred from the combined data (Grande, 1994; Chen et al., 2000, 2003; Chen, 2001). Separate analyses of independent partitions are an efficient way to assess the reliability of clades and to identify marker-specific reconstruction artifacts.

However, as mentioned above, keeping partitions separate has its own risks (see review in Miyamoto and Fitch, 1995; Lecointre and Deleporte, 2005). To circumvent these problems, it is interest-

Table 3
Characteristics of the datasets used in this study. The statistics were computed using p4 version 0.86.r43 (Foster, 2004, http://bmnh.org/pf/p4.html).

Number of sequences (new ones)		Rhodopsin	MLL	IRBP	RNF213
		190 (92)	165 (77)	161 (66)	118 (114)
Alignment length		856	730	828	991
Variable sites		572 (66.8%)	542 (74.2%)	684 (82.6%)	799 (80.6%)
Informative sites		469 (54.7%)	468 (64.1%)	557 (67.2%)	727 (73.3%)
Pairwise differences	Mean	0.214861	0.267751	0.225977	0.220434
	Minimum	0.007009	0.004644	0.013285	0.015228
	Maximum	0.857477	0.604380	0.524155	0.773604
P-value of χ^2 homogeneity tests	Global	0.000015	0.922810	0.614509	1.000000
	First codon	1.000000	1.000000	1.000000	1.000000
	Second codon	1.000000	1.000000	1.000000	1.000000
	Third codon	0.000000	0.000000	0.000000	0.117940
Location (*Tetraderon chromosome*)		9	10	2	3

ing to perform both separate and simultaneous analyses (Mickevich, 1978; Bull et al., 1993; Miyamoto and Fitch, 1995). (Dettaï and Lecointre, 2004 Fig. 2 therein), Dettaï and Lecointre (2005) and Li and Lecointre (2008) proposed partial combinations as a way to explore marker-specific topologies and to assess the reliability of clades. In their approach, not only is each elementary dataset analyzed separately, but every possible combination of the datasets is produced and analyzed too.

However, counting occurrences makes sense only when the trees taken into account are based on independent data. The minimal independent data units (elementary datasets) and their combinations are grouped into various sets of datasets: the partitioning schemes. A partitioning scheme, contains independent non overlapping datasets (elementary datasets or combinations thereof, see Li and Lecointre, 2008). For example, among all possible combinations of our datasets, RNF213 and the combination of the three other markers together form a partitioning scheme because the two parts do not contain elementary datasets in common. The number of clade occurrences may be then counted over the two trees obtained from these datasets.

In the present study, we used this approach, analyzing every possible combination of the datasets and recording repeated clades from combinations having no marker in common. This allows to take into account both the strengths and the weaknesses of separate and simultaneous analyses. The four nuclear markers were thus assembled in 15 combinations of one to four elementary datasets.

2.4. Datasets design

All genera for which we could obtain sequence data for at least one of the four nuclear markers were used in this study, in order to cover a broad taxonomic area, and because it has been shown that even a single sequence can still convey relevant information for the phylogenetic analyses (Wiens and Reeder, 1995). Nonetheless, missing data can sometimes disturb phylogenetic reconstruction, therefore, we made a decision about the minimum amount of sequences that need to be present for a taxon to be included in a dataset. The taxa for which half the markers (or more) were missing for a given combination were not included in that combination. This means that in a combination, a terminal must have sequences for at least two of the markers in a combination of 2 or 3 markers, and sequences for 3 or 4 markers for the combination of the 4 markers. For a few taxa, the sequences for different genes were obtained from different species of the same genus. Using such chimeric sequences at the species level for a study at the interfamilial level should not be problematic. For *Callionymus*, *Coryphaena* and *Nerophis*, species were not fused in a chimeric sequence because this would not have led to a better taxonomic overlap between the different markers: *Callionymus lyra* was present for the four markers while *C. schaapii* was present for Rhodopsin only, *Coryphaena equiselis* was present for the four markers while *C. hippurus* was present for IRBP only, and *Nerophis lumbriciformis* was present for RNF213, IRBP and Rhodopsin while *N. ophiodon* was present for IRBP only.

2.5. Primary analyses

Considering the taxonomic scale of our study, sequence data were analyzed under probabilistic sequence evolution models. PhyML (Guindon and Gascuel, 2003) was used for its speed, with a GTR + I + Γ model.

To offer an assessment of the role played by the RNF213 sequence data in the resolution of the 'acanthomorph bush', four trees were compared: the tree based on the new RNF213 sequence data, the tree based on the combination of the three other nuclear markers, the tree based on the combination of all four datasets (the 'total evidence' tree) and an MRP-like supertree displaying/summarizing the reliable clades calculated from the repetition indices of Li and Lecointre (2008), based on partial combinations and validity domains for the four datasets studied here.

2.6. Validity domains: adapting Li and Lecointre's method to datasets with different sets of taxa

To evaluate the reliability of clades, Li and Lecointre (2008) proposed repetition indices based on the partial combinations strategy (Dettaï and Lecointre, 2004). However, the proposed indices are only valid when all trees to be compared have the same set of terminals. Here, restricting all analyses to genera present in all four elementary datasets would have resulted in discarding nearly half the taxa, a considerable loss of information. To avoid this problem, we adopted here a pruning strategy based on three levels of what we call 'validity domains' (Fig. 1).

Analyses of the various dataset combinations were done on different sets of taxa, depending on the proportion of available sequences for a given taxon in the combined datasets. The sets of taxa included in each separate and combined analysis are called the 'first-level validity domains' (validity domains of the primary analyses). As stated earlier, we decided to take into account the taxa present in at least half the elementary datasets of a given combination. With three elementary datasets A, B and C, noting V_A, V_B and V_C their validity domains, the validity domain of $A \cup B \cup C$ would be:

$V_{A\cup B\cup C} = (V_A \cap V_B) \cup (V_A \cap V_C) \cup (V_B \cap V_C)$ (that is, the taxa that are either in A and B, in A and C or in B and C).

These validity domains are, logically, also the sets of leaves of the trees resulting from the primary analyses. The number of occurrences of the clades are counted over collections of such trees (see Fig. 1).

But a clade can be recognized and counted only when the trees are defined on the same set of taxa. As the count is performed within a partitioning scheme (a set of independent, non overlapping datasets, see above), the sampling for a given partitioning scheme has to be reduced to the taxa shared by all trees of the

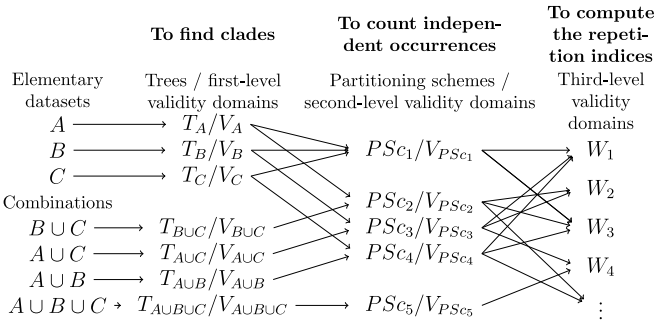

Fig. 1. The 3 levels of validity domains. The first-level validity domains (V_X) are the sets of leaves of the trees (T_X) obtained by the analyses of the datasets (X). In this example, 3 elementary datasets are used, which leads to 7 datasets, and thus to 7 trees and 7 first-level validity domains. The second-level validity domains (V_{PSc_i}) are the intersections of the validity domains of the independant datasets involved in the partitioning schemes (PSc_i). Here, only the full partitioning schemes are shown. The occurrences of the clades are counted within a partitioning scheme, across its constituent datasets, after pruning the corresponding trees of the taxa outside the relevant second-level validity domain. The third-level validity domains (W_i) are the intersections of all possible combinations of second-level validity domains. The repetition indices are attached to such third-level validity domains. They are based on the maximum number of occurrences (for the clades once pruned of the taxa outside the third-level validity domain) found among the partitioning schemes whose validity domains span at least the entire third-level validity domain. Only some of the possible third-level validity domains are shown here.

scheme. This is a 'second-level validity domain'. It is associated to the partitioning scheme through a process we call 'prune-to-count'. Taxa that are not in all datasets in the partitioning scheme are pruned from the trees. If we note PSc_2 partitioning scheme $(A, B \cup C)$, the corresponding second-level validity domain (Fig. 1) would be:

$$V_{PSc_2} = V_A \cap V_{B \cup C}.$$

In addition to using the definition of partitioning schemes of Li and Lecointre (2008), we also took into account all the 'partial partitioning schemes' (not shown in Fig. 1). These do not include all elementary datasets but have a larger second-level validity domain (a larger shared taxonomic sampling) than full partitioning schemes. This has the advantage of retaining more information about potentially reliable relationships.

The repetition index for a clade (Li and Lecointre, 2008) involves a comparison between the best number of occurrences of the clade across all possible partitioning schemes and the best number of occurrences of its contradictors.

But here, different partitioning schemes (PSc_1, PSc_2, PSc_3, etc.) can have different taxonomic samplings. The repetition index could be computed in the set of taxa common to all partitioning schemes, but this would entail an important loss of terminals. Therefore, the repetition index was also computed using all possible smaller sets of partitioning schemes, which potentially have a higher number of shared terminals.

Computing a repetition index which takes into account a given set of partitioning schemes, requires restricting the analysis (in terms of terminals) to the intersection of the validity domains of these partitioning schemes.

This second pruning step is performed in order to be able to compare clades from the different partitioning schemes of the set. We call it a 'prune-to-compare' process: if PSc_1, PSc_3 and PSc_4 are the partitioning schemes from which the clades to be compared are drawn, the comparison is made in a 'third-level validity domain' (noted W_1, Fig. 1):

$$W_1 = V_{PSc_1} \cap V_{PSc_3} \cap V_{PSc_4}.$$

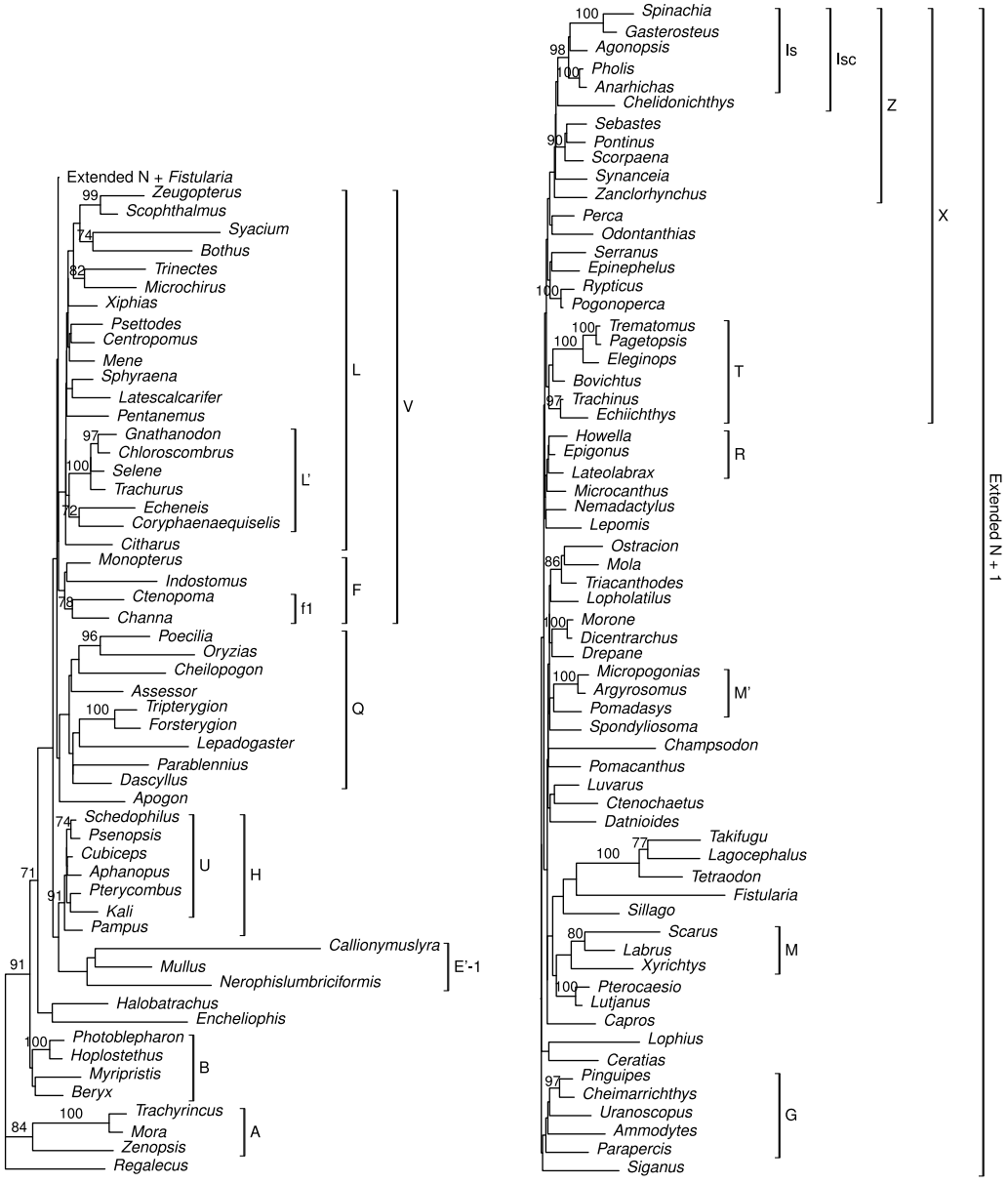

Fig. 2. Maximum likelihood tree obtained by the analysis of the new RNF213 sequence data matrix under a GTR + I + Γ model with phyML Guindon and Gascuel (2003). Bootstrap proportions are reported for clades over 70%.

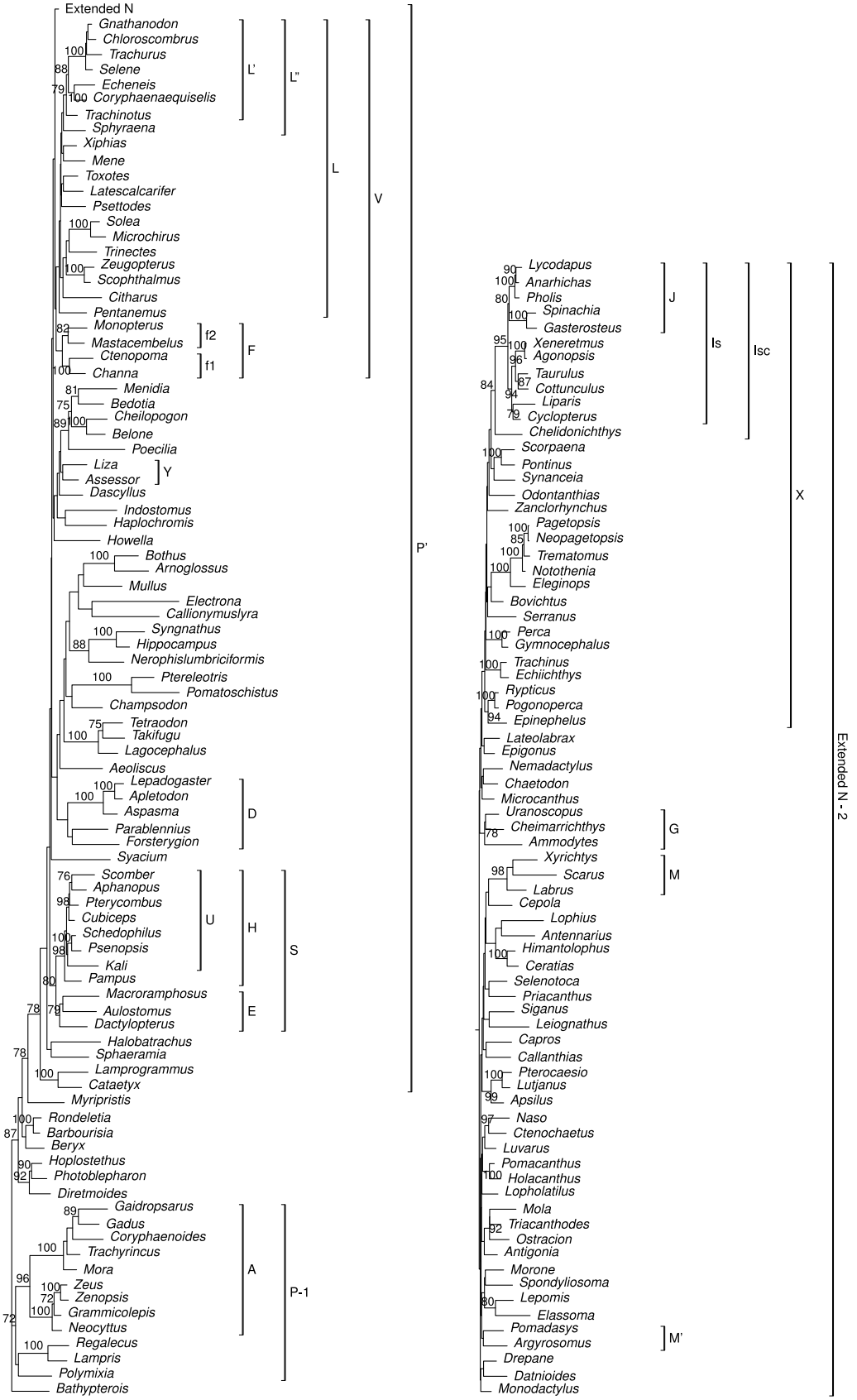

Fig. 3. Maximum likelihood tree obtained by the analysis of the combined matrix Rhodopsin + MLL + IRBP under a GTR + I + Γ model with phyML Guindon and Gascuel (2003). Bootstrap proportions are reported for clades over 70%.

Table 4
Clades of interest extracted from the separate and multiple combined analyses and repetition index. New names are proposed for some of those reliable clades of the 'acanthomorph bush'. First column lists the contents of the clade; the name given to the clade refers to the last common ancestor to the taxa indicated. Second column indicates by a cross the presence of the clade in Fig. 2. A blank means that the clade is not recovered in the tree Fig. 2 and a question mark indicates that the presence of the clade cannot be assessed either because of an incomplete taxonomic sampling or because of irresolution. Third column indicates presence of clades in Fig. 3. Fourth column indicates presence of clades in Fig. 4. The mention 'x − 1' indicates that a single taxon escapes from the clade (generally a long branch). Fifth column indicates presence of the clade in the summary tree of Fig. 5. Sixth column gives the letter associated to the clade in Chen et al. (2003) and Dettaï and Lecointre (2005, 2008) and proposes letters for new clades (P, P′, R, S, T, U, V, W, Y, Z, L′, L″, M′, M″). Seventh column refers to the presence of the clade in the study of Dettaï and Lecointre (2008) based on the IRBP gene. Eighth column records the clade in the studies of Miya et al. (2003, 2005) based on independent mitochondrial sequence data; ninth column in the study of Mabuchi et al. (2007) using the same genes as in Miya et al. (2005) and tenth column in the study of Kawahara et al. (2008) also based on the same markers. Eleventh column records the clades in the study of Smith and Craig (2007) based on mitochondrial and nuclear data independent from both Dettaï and Lecointre (2005) and Miya et al. (2005). In these last five columns, question marks are given either when taxonomic sampling is insufficient or the interrelationships unresolved. The last column proposes a name to some of the clades that have been repeatedly found in several previous studies, or reliable clades newly identified by the present study.

Last common ancestor to	Fig. 2	Fig. 3	Fig. 4	Fig. 5	Nomenclature (Chen et al. and this study)	Dettaï and Lecointre (2008)	Miya et al. (2003, 2005)	Mabuchi et al. (2007)	Kawahara et al. (2008)	Smith and Craig (2007)	Names (new ones in bold)
Zeioidei, Gadiformes	x	x	x	x	A	x	x	?	?	?	**Zeioigadiformes**
Zeioidei, Gadiformes, Polymixiiformes	?				O	x		?	?	?	
Lampridiformes, Percopsiformes	?	?	?	x		x		?	?	?	
Lampridiformes, Percopsiformes, Polymixiiformes	?	?	?	x				?	?	?	
Zeioidei, Gadiformes, Polymixiiformes, Lampridiformes, Percopsiformes	?	?	?	x	P	x		?	?	?	
Trachichthyoidei, Berycoidei, Holocentroidei	x				B		x	?	?	?	Beryciformes (after Chen et al., 2003)
P sister-group of the rest of acanthomorpha	?	x	x	x		x	?	?	?	?	
Ophidiiformes sister-group of non-P and non beryciform and non Stephanoberyciformes acanthomorphs		x	x	x	P′	?	x	x	x	?	Percomorpha (*sensu* Miya et al., 2003)
Mugiloidei, Atherinomorpha	?				C	?	?			?	
Blennioidei, Gobiesocoidei	?	x	x	x	D	x	x	x	x	?	**Blenniiformes**
Mugiloidei, Plesiopidae	?	x	x	x	Y	?	?	?	?	?	
Mugiloidei, Plesiopidae, Blenniiformes, Atherinomorpha, Cichlidae	x		x	x − 1	Q	x	x?	x?	B?	x?	**Stiassnyiformes**
Apogonidae, Gobioidei				x	W	?	?	?	?	?	
Syngnathidae, Callionymoidei, Mullidae	x		x		E′	?	?	?	?	?	
Centrolophidae, Bramidae, Nomeidae, Scombridae, Trichiuridae, Chiasmodontidae	x	x	x		U	?	?	?	?	?	
Stromateidae, Centrolophidae, Bramidae, Nomeidae, Scombridae, Trichiuriae, Chiasmodontidae	x	x	x	x	H	x	?	?	?	x?	**Stromateoidei**, new definition
Dactylopteridae, Aulostomidae, Macrorhamphosidae	?	x	x	x − 1	E	?	?	?	x		
Stromateoidei + E	?	x	x	x − 1	S	?	?	?	?		
Channidae, Anabantidae	x	x	x	x	f1	x	?	?	?	?	Labyrinthoidei
Symbranchidae, Mastacembelidae	?	x	x	x	f2	x	x	x	A?	?	Synbranchiformes
Channidae, Anabantidae, Mastacembelidae, Symbranchidae, Indostomidae	x	x	x	x	F	x	?	?	A?	?	**Anabantiformes**
Uranoscopidae, Ammodytidae, Cheimarrichthyidae, Pinguipedidae	x	x	x	x	G	x	?	?	?	x?	**Paratrachinoidei**
Sciaenidae, Haemulidae	x	x	?	x	M′	?	?	?	?		
Centrarchidae, Moronidae, Elassomatidae				x	M″	?	?	?	?		
Cottoidei, Zoarcoidei					I	x				x	
Zoarcoidei, Gasterosteidae		x	x	x	J	?	x	x	x		**Zoarciformes**
Cottoidei, Zoarcoidei, Gasterosteidae	x	x	x	x	Is	?	x	x	x	x	**Cottimorpha**
Cottoidei, Zoarcoidei, Gasterosteidae, Triglidae	x	x	x	x	Isc	?	x	?	?	x	**Triglimorpha**
Cottoidei, Zoarcoidei, Gasterosteidae, Triglidae, Scorpaenidae, Sebastidae, Synanceiidae, Congiopodidae	x		x	x	Z	?	?	?	?		
Notothenioidei, Percophidae	?	?	?				?	?	?	F	Notothenioidi Smith and Craig (2007)
Notothenioidi, Niphon, Acanthistius, Percidae							?	?	?	E	Percoide
Notothenioidei, Trachinidae	x		x	x − 1	T		?	?	?		

(*continued on next page*)

Table 4 (*continued*)

Last common ancestor to	Fig. 2	Fig. 3	Fig. 4	Fig. 5	Nomenclature (Chen et al. and this study)	Dettaï and Lecointre (2008)	Miya et al. (2003, 2005)	Mabuchi et al. (2007)	Kawahara et al. (2008)	Smith and Craig (2007)	Names (new ones in bold)
Notothenioidei, Percidae					K		?	?	?		
Notothenioidei, Percidae, Triglimorpha, Trachinidae, Scorpaenidae, Sebastidae, Synanceiidae, Serranidae, Congiopodidae	x	x	x	x − 1	X	x	?	?	G?	x	**Serraniformes**
Carangoidei stem group of Echeneidae and Coryphaenidae	x	x	x	x	L′	x	?	?	?	?	
Sphyraenidae sister-group of L′		x	x	x	L″	?	?	?	?		
Pleuronectiformes, Centropomidae, Carangidae, Coryphaenidae, Menidae, Sphyraenidae, Polynemidae, Echeneidae, Toxotidae, Xiphiidae	x	x	x − 1	x − 1	L	x	x?	x?	E?	x?	**Carangimorpha**
Carangimorpha, Anabantiformes	x	x	x		V	?	?	?		?	
Tetraodontiformes, Lophiiformes, Caproidei, Elassomatidae, Acanthuridae, Siganidae, Pomacanthidae, Drepanidae, Chaetodontidae	?				N	x	x?	x?	H?	?	
Extended N	x + 1	x − 2	x − 1			x?	x?	x?	H + G?		
Labridae, Scaridae	x	x	x	x	M	x	?	x	?	?	Labroidei *sensu stricto* **Epigonoidei**
Percichthyidae, Epigonidae, Lateolabracidae	x		x	x	R	?	?	?	?	x	

This pruning and comparing step is done for all combinations of partitioning schemes and leads to several third-level validity domains (W_1, W_2, W_3, etc. Only some of them are represented in Fig. 1).

Thus, within each W, each clade has a first order repetition index, which is the maximum number of occurrences found among the involved partitioning schemes by counting all clades corresponding to the clade under focus before the pruning process. Then, the best first order repetition index found among the contradictors of the clade under focus within the same W is subtracted from this first order repetition index as described in Li and Lecointre (2008). This procedure associates a repetition index to each clade, each association being defined in a particular W.

The procedure can be summarized as follows (see also Fig. 1):

1. Analyze each dataset (elementary datasets and all possible combinations thereof).
2. Arrange the data into partitioning schemes (sets of independent datasets) and, for each of them, determine the corresponding validity domain (set of included terminals). The validity domain of a partitioning scheme (second-level validity domain, noted V_{PSc}) is the intersection of the validity domains of its constituent datasets (first-level validity domains, noted V).
3. For each partitioning scheme, prune the taxa not in the validity domain of the partitioning scheme from the trees and record the clades in the pruned trees with their number of occurrences (whenever a number of clade occurrences is used, a sum of support values could be used instead).
4. Combine the partitioning schemes and determine the validity domain of each of the possible combinations (third-level validity domains, noted W). The validity domain of a combination of partitioning schemes is the intersection of the validity domains of its constituent partitioning schemes. Group together combinations that have the same validity domain.
5. For each of the preceding validity domains (W), prune the taxa that are not in the validity domain from the clades found in the associated combinations of partitioning schemes. For each distinct resulting clade, keep as first order repetition index the best number of occurrences found among the clades that, once pruned, become the clade under focus.
6. Within each third-level validity domain, proceed as in Li and Lecointre (2008) to obtain the final repetition indices.

In order to take robustness into account, the repetition index can also be based on sums of bootstrap proportions instead of sums of occurrences. In the present reliability analyses, to accommodate for the uncertainty entailed by the use of heavy heuristics, bipartition occurrences were weighted by their bootstrap supports across 100 resamplings. But pruning taxa from a tree causes the fusion of several internal branches. The highest bootstrap support among fused branches was used to weight the bipartition delimited by such fused branches. We consider this choice justified because in order to collapse a clade, one must break its branch. The clade resulting from taxon pruning in a restricted validity domain is the 'heir' of one or more pre-pruning clade(s), as they differ only with respect to the terminals that have been pruned. This new clade may thus be supported by several successive branches in the original tree, each of which has to be broken. This clade can therefore be considered to be as strong as the strongest of its 'ancestors' in the original trees.

2.7. Displaying reliable clades

Some clades repeated in the separate analyses can be absent from the tree based on all available data. This has been shown theoretically (see the clade BCD in Barrett et al., 1991, Fig. 1) as well as

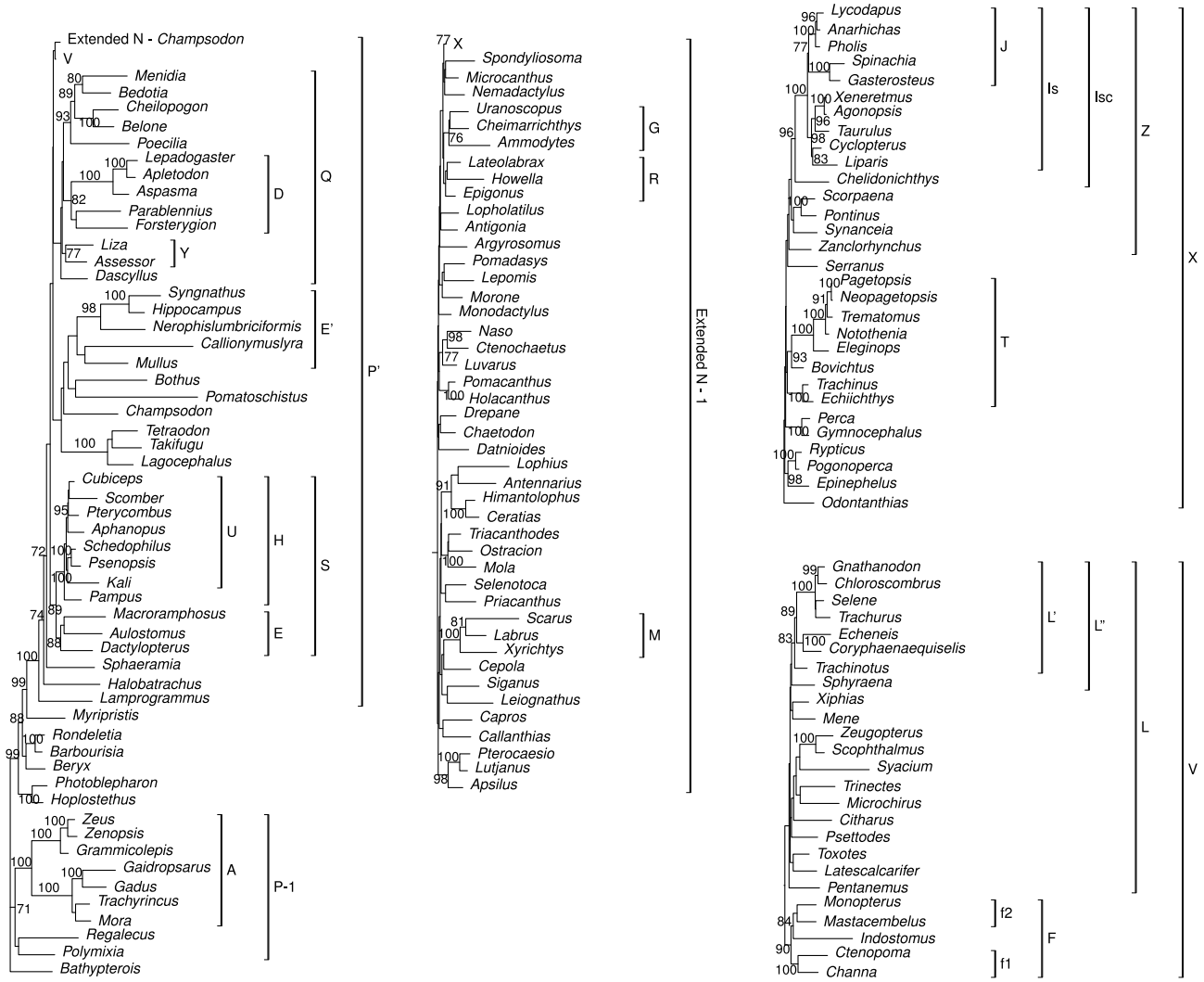

Fig. 4. Maximum likelihood tree obtained by the analysis of the combined matrix of the four nuclear genes ('total evidence') under a GTR + I + Γ model with phyML (Guindon and Gascuel, 2003). Bootstrap proportions are reported for clades over 70%.

empirically (Dettaï and Lecointre, 2004, Figs. 4 and 5 therein). This is one of the grounds to conduct both separate and simultaneous analyses (Nixon and Carpenter, 1996). A tree summarizing the clades considered reliable has to be constructed to allow the visualization of the possible discrepancies. To synthesize the results of the reliability analysis, we used a supertree approach derived from the MRP method (Baum and Ragan, 2004): the bipartitions with positive repetition indices from the various third-level validity domains were gathered in a matrix representation and weighted by their repetition indices. This matrix was analyzed under maximum parsimony.

3. Results

3.1. Effect of RNF213 on support

Fig. 2 is the tree based on RNF213 sequence data only. The marker allows to recover clades already recorded in previous molecular phylogenies (Dettaï and Lecointre, 2005, 2008, Table 4), namely A, D, E′, F, G, H, E′ + H, L, M, Q, X, Is, Isc, P (Zeioidei, Gadiformes, Polymixiiformes, Percopsiformes and Lampridiformes, as in Dettaï and Lecointre, 2008, submitted for publication).

Clade N (Dettaï and Lecointre, 2005, 2008; Yamanoue et al., 2007; Kawahara et al., 2008; Holcroft and Wiley, 2008) fails to appear. Lophiiforms and *Siganus* are out of it, though without resolution. Resolution inside N is also very poor. Clade B is the monophyly of Beryciformes *sensu lato* (Chen et al., 2003; Miya et al., 2005), however that clade is not repeated throughout studies. Clades C and O are not recovered because of incomplete taxonomic samplings, while clades I, J, K are contradicted.

Comparing Fig. 3 (combination of Rhodopsin, MLL and IRBP) to Fig. 4 (combination of all four markers), it is not clear whether RNF213 sequence data are able to improve resolution. More investigation is needed to establish whether clade N should also include (as in Fig. 3) Monodactylidae and Lutjanidae (they should according to Yamanoue et al., 2007; Holcroft and Wiley, 2008), Leiognathidae, Cepolidae, Labridae, Scaridae and Moronidae (the last three are closely related in Dettaï and Lecointre, submitted for publication), Centrarchidae, Elassomatidae (as suggested in Dettaï and Lecointre, submitted for publication), Callanthiidae, Priacanthiidae, Caesionidae, Malacanthidae, Datnioididae, and Scatophagidae, Sciaenidae and Haemulidae (as in Chen et al., 2007). The previously described clade N plus the families listed above constitute a working hypothesis that we call here 'extended N'. That clade is rendered paraphyletic in Fig. 4 ('total evidence') and Fig. 5 (supertree based on reliability indices). If those topologies are to be trusted, it could be extended again to contain Kyphosidae, Aplodactylidae, Cheilodactylidae, Sparidae, Champsodontidae and clades X, G and R.

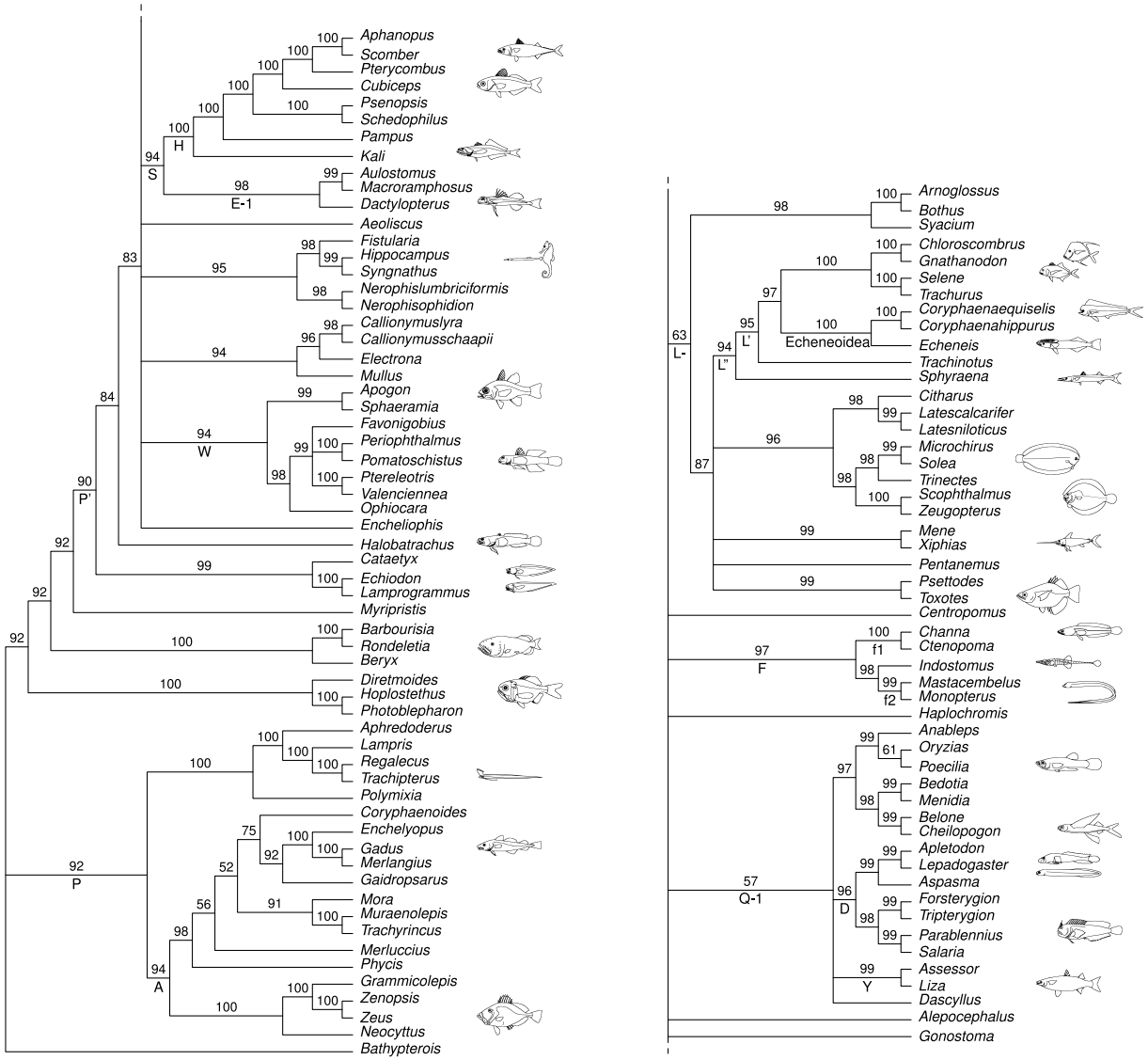

Fig. 5. Supertree exhibiting the clades having the highest repetition indices (Li and Lecointre, 2008) in the partial combination and validity domains approach. The tree is the majority-rule consensus of the most parsimonious trees obtained by 10,000 RAS + TBR parsimony analyses by PAUP* (Swofford, 2002) of the matrix representing the clades with positive repetition indices, weighted by their repetition indices. The values above the branches are the percentages of equally parsimonious trees that include the clades. The illustrations come from Fishbase (Froese and Pauly, 2006).

In Figs. 3 and 4, clade H is the sister-group of clade E (forming together clade S) while clade H is the sister group of E′ in Fig. 2 (RNF213 data only). This E′ + H clade might be due to the lack of taxa of clade E in the RNF213 dataset.

3.2. New results from RNF213 sequence data

The new RNF213 sequence data adds some interesting results, while others come from the addition of new taxa to the previously published samplings.

The ability of RNF213 sequence data to get more clades can be assessed through clades absent from Fig. 3 and present in Figs. 2 and 4:

- Clade Q (Dettaï and Lecointre, 2005, 2008) is recovered (Gobiesociformes, Blennioidei, Atherinomorpha, Mugiloidei, Pomacentridae) with a new member, the Plesiopidae;
- Family Plesiopidae is in clade C, probably as sister-group to the Mugiloidei;
- Clade E′: Mullidae, Callionymidae, Syngnathidae. That clade is not new, already proposed in Dettaï and Lecointre (submitted for publication) and not contradicted by Kawahara et al. (2008) because of poor support within their clade ‘D’ and absence of any mullid or callionymid;
- Clade R: Howellidae, Lateolabracidae and Epigonidae. It was already present in Smith and Craig (2007);
- Clade T: Notothenioidei, Trachinidae due to the addition of *Echiichthys*;
- Clade Z: Cottoidei, Zoarcoidei, Gasterosteidae, Triglidae, Scorpaenidae, Sebastidae, Synanceiidae, Congiopodidae. That clade is a beginning of structuration within clade X (Dettaï and Lecointre, 2004).
- Clade S (E + H) because members of E are present in Figs. 3 and 4;
- Indostomidae is a member of clade F because *Indostomus* is added (also found by several studies, Miya et al., 2003, 2008);
- Clade U: *Pampus* (Stromateidae) sister-group of all other members of H in Figs. 2–4;

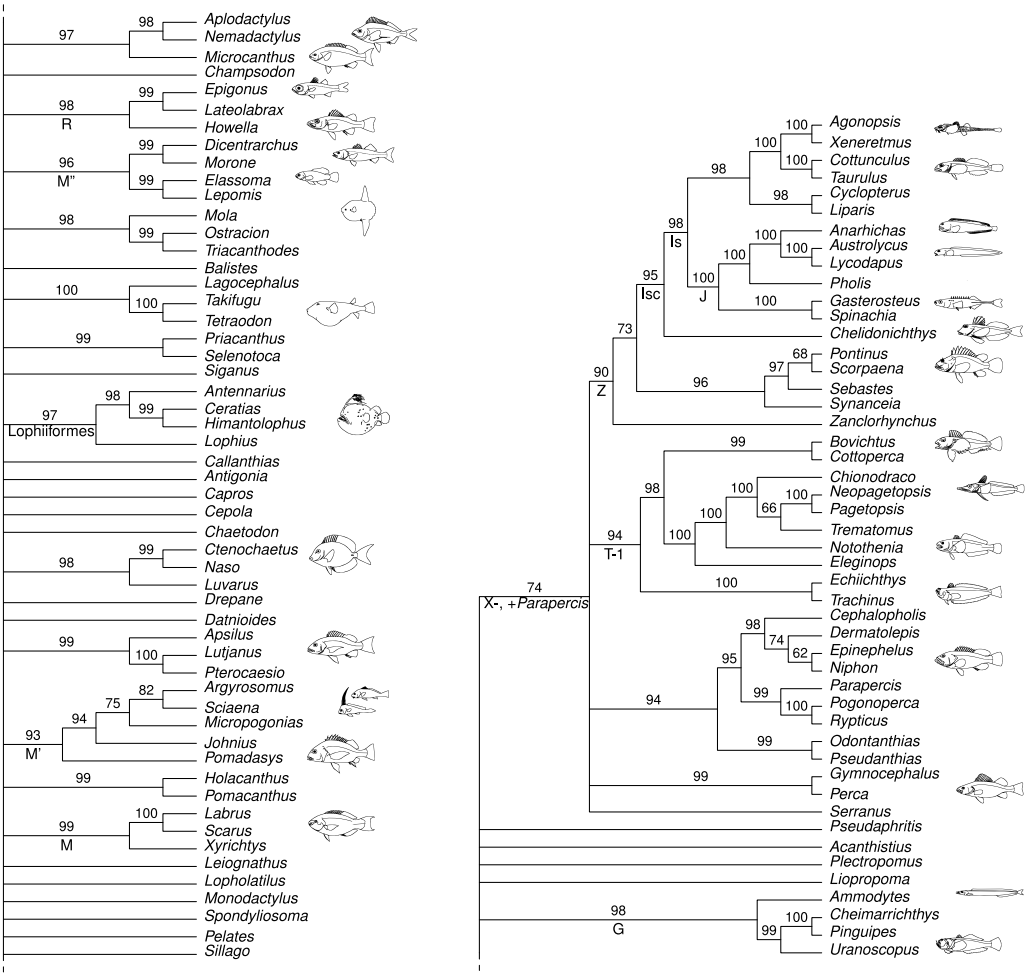

Fig. 5. (*continued*)

- Clade V: L + F in Figs. 3 and 4;
- Clade L′: Coryphaenidae and Echeneidae nested within the Carangidae.

Fig. 5 is the supertree summarizing the reliable clades. When this tree is compared to Fig. 2, it appears that some of the new clades listed above were recovered by RNF213 only.

- Clade R: Epigonidae, Lateolabracidae and Howellidae form a clade (as in Smith and Craig, 2007);
- Indostomidae is a member of clade F (as in Miya et al., 2003; Kawahara et al., 2008);
- Clade Q including the Plesiopidae;
- Clade T (Notothenioidei, Trachinidae, contradicting the clade K of Dettaï and Lecointre (2004, 2005).

These clades are an indication that the new marker has the potential to help to the emergence of some not yet identified reliable clades, while it also has the potential to recover clades previously recorded as reliable, like A, D, Q, H, f1, f2, F, G, Is, Isc, X, L, M.

The comparison of Fig. 5 with Fig. 4 is interesting to evaluate whether there are reliable clades that do not appear in the tree based on the simultaneous analysis of all datasets ('total evidence'). It is indeed the case for the following clades:

- Clade W: Apogonidae and Gobioidei;
- Clade M′: Sciaenidae and Haemulidae;
- Clade M″: Centrarchidae, Moronidae and Elassomatidae;

This discrepancy has already been described (Dettaï and Lecointre, 2004), and is not entirely surprising as the tree based on the whole data can be perturbed by the usual pitfalls of phylogenetic reconstruction like any other tree.

Symmetrically, some clades from the total evidence approach are not found in Fig. 5:

- Clade E′ (Figs. 2 and 4);
- Clade U (Figs. 2–4);
- Clade V (Figs. 2–4);

These clades are intuitively more problematic because they are found from different trees based on independent data. Clades U and V are striking examples. They are repeated from independent data (Fig. 2: RNF213 data only, and Fig. 3: all other data) while they are not recovered using the multiple combinations protocol.

4. Discussion

4.1. New names for new reliable clades

A number of clades had already been recovered in the previous studies and will not be further discussed (Chen et al., 2000, 2003; Dettaï and Lecointre, 2004, 2005, 2008, submitted for publication): A, C, D, E, F, G, H, J, K, L, N, M, P′. We will focus here on the new results. In both cases, new names are proposed for some of these clades (Table 4)

- Clade Y: Plesiopids (roundheads) are the sister-group of the Mugiloidei (grey mullets). This has not been proposed before, and was not found by Smith and Craig (2007), as they had no mugiloid included.
- The large clade Q contains the Mugiloidei (grey mullets), the Plesiopidae (roundheads), the Atherinomorpha (guppies, pupfishes, silversides, needlefishes), the Pomacentridae (damselfishes), the Blennioidei (blennies) and the Gobiesociformes (clingfishes). The group was present with a more reduced sampling in Chen et al. (2003) and Miya et al. (2005), as there were no cichlid, no pomacentrid and no plesiopid; Dettaï and Lecointre (2005) added a cichlid but no pomacentrid and no plesiopid. Different studies showed that the Cichlidae were close to a group containing the Atherinomorpha (Chen et al., 2003, 2007; Dettaï and Lecointre, 2005; Mabuchi et al., 2007) and not to the other members of the six-family labroidei: Labridae and Scaridae (Dettaï and Lecointre, 2005; Mabuchi et al., 2007; Chen et al., 2007). Among these studies, the best taxonomic sampling is reached by Mabuchi et al. (2007) showing that the Pomacentridae, the Embiotocidae (surfperches) and the Cichlidae are close to each other (their clade 'B') and to members of what we call here clade Q, while the Odacidae (cales), the Scaridae (parrotfishes) and the Labridae (wrasses) form a clade (their clade 'A') and are members of what we call here the 'extended clade N′. These results are clearly corroborated by Chen et al. (2007) from independent nuclear and mitochondrial sequence data. The Labroidei are therefore diphyletic and the specialized 'labroid' pharyngeal jaw apparatus evolved twice. Here the cichlids (*Haplochromis*) have an undetermined position within clade Q, while the Blennioidei are the sister-group of the Gobiesociformes (clade D, Chen et al., 2003). It must be noticed that the family Pseudochromidae (dottybacks) may also be a member of clade Q according to the position of *Labracinus* in the tree of Mabuchi et al. (2007). This is corroborated by the tree of Smith and Craig (2007) where another pseudochromid, *Pseudochromis*, lies within a clade corresponding to the present clade Q (Cichlidae, Blennioidei, Atherinomorpha). But gobiesociforms and mugiloids are absent in their dataset and some families missing from ours integrate their equivalent of clade Q: Opisthognathidae (jawfishes), Grammatidae and Pholidichthyidae. An interesting feature emerges from the comparison of all these studies. Clade Q may contain the Atherinomorpha, the Mugiloidei, the Plesiopidae, the Pomacentridae, the Cichlidae, the Embiotocidae, the Blennioidei, the Gobiesociformes, the Pseudochromidae, the Opisthognathidae, the Grammatidae and the Pholidichthyidae. A closer look for possible morphological characters uniting all these taxa yielded one candidate. Mooi (1990) records adhesive chorionic filaments arranged around the micropyle of the demersal egg in grammatids, opisthognathids, pomacentrids, plesiopids and apogonids (the latter is not in Q here but in clade W, see page 21). Such eggs are found in pseudochromids (Mooi, 1993) and in plesiopids *sensu lato* (i.e. including acanthoclinids Mooi, 1993 and notograptids Gill and Mooi, 1993). Gill and Mooi (1993) also record such demersal eggs with filaments in blennioids (here clade Q) and gobioids (here in clade W), as did Breder and Rosen (1966). Parenti (1993) records these eggs as a synapomorphy of the Atherinomorpha (viviparity in that group being a derived condition). Additionally Smith and Wheeler (2004) mention these eggs in the Cichlidae, and Breder and Rosen (1966) in the Gobiesocidae and the Kurtidae (probably in clade W). These eggs are recorded in 9 of the 12 potential components of clade Q. The Mugiloidei and the Embiotocidae do not have these eggs (Breder and Rosen, 1966), but these conditions may be reversals, as mugiloids are the sister group of plesiopids and embiotocids are grouped with cichlids and pomacentrids. Demersal eggs with filaments may therefore be a synapomorphy of the clade. The presence of this character state also in gobioids, kurtids and apogonids remains to be explained. It could have been gained by convergence, but this needs an in-depth comparison to explore the homology in and between these two groups. Alternatively, demersal eggs with chorionic adhesive filaments could also be a synapomorphy of a clade W + Q, however more resolution is needed to test that hypothesis.
- Clade W: Apogonidae (cardinalfishes) are closely related to the Gobioidei in our Fig. 5 (as in Smith and Wheeler, 2006), while *Apogon* is grouped with *Kurtus* in Smith and Craig (2007) in the absence of gobioids. *Kurtus* is found to be the sister-group of *Apogon* and gobies in Smith and Wheeler (2006). Interestingly, horizontal and vertical rows of sensory papillae on the head and body are exclusively shared by Apogonidae, Kurtidae (nurseryfishes), Gobioidei (gobies) and Champsodontidae (crocodile toothfishes) (Johnson, 1993, p. 18). However, here *Champsodon* fails to cluster with the apogonid and gobioidei representatives. On the basis of anatomical data, Prokofiev (2006) stresses a close relationship between the Apogonidae and the Kurtidae (without mentioning the Gobioidei). Comparison of different studies and Smith and Wheeler (2006) suggest that a clade 'W' at least composed of Apogonidae, Kurtidae and Gobioidei is worth being investigated further. Like clade Q, this clade would also be supported by the presence of eggs with chorionic adhesive filaments (see page 20). Apogonids and kurtids were not among the potential sister-groups of the Gobioidei identified by Winterbottom (1993): trachinoids, gobiesocoids, hoplichthyids and other scorpaeniforms. However, apogonids and kurtids were not included in his study.
- Clade T (notothenioids more closely related to trachinids than to percids) contradicts the clade K of Chen et al. (2003) and Dettaï and Lecointre (2004, 2005) where the perches (Percidae) are the most closely related group to Antarctic fishes (Notothenioidei). Nonetheless, in Chen et al. (2003) as well as in Dettaï and Lecointre (2004, 2005), *Trachinus* (Weeverfish) was always placed very close to clade K. Interestingly, in Smith and Craig (2007) *Bembrops* (Percophidae), *Acanthistius* (Serranidae, Anthiinae) and *Niphon* (Serranidae, Epinephelinae) are inserted between percids and notothenioids and *Trachinus* is branched off far away, among serranids. On the contrary, in Smith and Wheeler (2006) trachinids are more closely related to notothenioids than percids, while *Bembrops* is still the closest to notothenioids. In our summary tree (Fig. 5), *Niphon* is among serranids and *Acanthistius* has an undertermined position. Sequence data for the genes analyzed here would be much needed for *Bembrops*, to test their effects on the relative positions of trachinids and percids and get a clearer idea about the sister-group of notothenioids.
- Clade Z is providing more precision within clade X: Synanceiidae (stonefishes), Scorpaenidae (scorpionfishes and rockfishes), Congiopodidae (pigfishes) and Sebastidae (thornyheads) constitute the stem-group of clade Isc. Clade Z cannot be identified in most other studies because of insufficient taxonomic sample overlap. In Smith and Craig (2007) the clade is very well represented by 33 terminals however it is not recovered because the Synanceiidae branches outside it and a clade made of the Bembridae (deepwater flatheads), Plectrogeniidae, and their 'clade E' (notothenioids, percids, percophids, anthines) is included in it. It is important to note that we have identified clade X and clade Z without taking into account single unstable taxa 'escaping' with no determined position. In fact, the problematic four taxa (*Acanthistius*, *Pseudaphritis*, *Liopropoma*, *Plectropomus*) have sequences for one marker only and have question marks for all the other genes. More data are needed to stabilize their position. Moreover, the pinguipedid *Parapercis* (grubfishes and sandperches)

is nested among serranids in Fig. 5. In Smith and Craig (2007) it is close to other trachinoid families like Ammodytidae (sandlances) and Cheimarrichthyidae (torrentfish), like in our Fig. 2. The position of *Parapercis* in Fig. 5 must be taken with caution. Indeed, clade G includes *Pinguipes* in Fig. 5 (along with three formerly 'trachinoid' families Ammodytidae, Uranoscopidae (stargazers), Cheimarrichthyidae) and in Fig. 2 the two pinguipedids *Pinguipes* and *Parapercis* are both placed in clade G. More sequence data is needed for *Parapercis* before a conclusion can be drawn on the mono- or polyphyly of the Pinguipedidae.

- Clade S (H and E) is recovered in Figs. 3–5; it does not appear in other studies because of the lack of overlap between the taxonomic samplings. In Chen et al. (2007), there is a 'backbone' of clade E′ + H with *Mullus* (E′) associated to *Scomberomorus* and *Psenopsis* (H). The study of Kawahara et al. (2008) dealing with the polyphyly of the Gasterosteiformes from independent sequence datasets using a complete sampling of that order at the family level includes no member of our 'clade H'. Moreover the position of their 'clade C' (containing *Macrorhamphosus*, *Aulostomus* and dactylopterids) is poorly supported, leaving the question open.
- The Gasterosteiformes are polyphyletic, with indostomids (armored sticklebacks) within clade F (with synbranchiformes) and gasterosteids (sticklebacks) closely related to the Zoarcoidei (eelpouts), a result fully confirmed by independent data in Miya et al. (2003) and in Kawahara et al. (2008) with a much larger sampling for gasterosteiform. In Kawahara et al. (2008), the Syngnathoidei are paraphyletic, including dactylopterids (flying gunards). Gasterosteoids are closer to the Zoarcoidei and indostomids closer to symbranchiforms. Interestingly, here, part of the Syngnathoidei (*Macrorhamphosus* and *Aulostomus*) are close to the Dactylopteridae (clade E) however other syngnathoids (*Aeoliscus*, *Syngnathus*, *Hippocampus* and *Nerophis*) never group with them, probably because they have long branches. Though they concluded from comparative anatomy and bone development that indostomids were gasterosteoid gasterosteiforms, Britz and Johnson (2002) mentioned a feature that is shared by indostomids and mastacembelids (though also by most other gasterosteoids): the lack of distal radials in all pterygiophores supporting fin spines at all developmental stages.
- Clade M′ (Sciaenidae (croakers) and Haemulidae (grunts)) has not been found by molecular studies because of lack of representatives included for these families. However, Smith and Craig (2007) did sample those two families but they do not appear related to each other in their tree. Also, from partially independent sequence data in Chen et al. (2007), haemulids appear close to lutjanids and sparids while sciaenids are closer to drepanids and chaetodontids.
- The same applies for clade M″ grouping the Centrarchidae (sunfishes), the Moronidae (temperate basses) and the Elassomatidae (pygmy sunfishes). Moreover, that clade contradicts the association of the Moronidae in Dettaï and Lecointre (submitted for publication) with some members of the labroids (i.e. labrids and scarids) and some members of the polyphyletic trachinoids. In Chen et al. (2007), *Elassoma* is not related to moronids and this family is closer to labrids and scarids. Clade M″ should be evaluated again with more taxa.
- Clades L′ and L″ are structuring the inside of clade L. Carangids (jacks and pompanos) are placed as the stem group of the Echeneoidea (*sensu* Johnson, 1993), represented here by Echeneidae (remoras) and Coryphaenidae (dolphinfishes). The Sphyraenidae (barracudas) are the sister-group of carangoids (carangids plus Echeneoidea). Johnson (1984, 1993) defined the Carangoidei as the Carangidae, Echeneidae, Rachycentridae, Nematistiidae and Coryphaenidae. Those clades L′ and L″ have not been found by previous molecular studies because of the lack of representation of these groups. The exception is Smith and Wheeler (2006), who confirm these two clades. Smith and Craig (2007) did find an equivalent of L but did not find any clade compatible with clade L″ as the Sphyraenidae are branched well within L.
- Clade R: *Epigonus*, *Howella*, and *Lateolabrax* form a clade (already found by Smith and Craig (2007)) suggesting close relationships of *Howella*, Lateolabracidae (Asian seaperches) and Epigonidae (deepwater cardinalfishes). Interestingly, the study of Smith and Craig (2007) includes other percichthyid genera (namely *Bostockia*, *Gadopsis*, *Macquaria*, *Nannoperca*), but *Howella* is not grouped with them but within their equivalent of clade R, suggesting the polyphyly of the Percichthyidae. This would not be surprising as the family is known to be poorly defined (Nelson, 1994). Prokofiev (2007) even erected a new family with three genera (Howellidae) on the basis of several osteological features. Other families like Polyprionidae (wreckfishes), Dinolestidae (long-finned pike), Pentacerotidae (armorheads), Acropomatidae (lanternbellies) appear in Smith and Craig (2007) as more closely related to the clade grouping *Howella*, *Epigonus* and *Lateolabrax* than *Howella* is to the other Percichthyidae. Sequence data for more markers from all those key taxa would be of interest to confirm the polyphyly of the Percichthyidae.
- Clade P is interesting. As a large clade located at the base of the acanthomorph tree, it has been difficult to find because of long-branch attractions in molecular studies of acanthomorph phylogeny. Long-branch attractions tend to attract the longest branches towards the outgroups (which have long branches by definition, see for example Dettaï and Lecointre, 2005) and create comb-like tree shapes at the most basal parts of the trees. Clade P groups Polymixiiformes (beardfishes), Percopsiformes (trout-perches), Lampridiformes (oarfishes and opahs), Zeioidei (dories), and Gadiformes (cods). The clade appears in Dettaï and Lecointre (2008) and is only partial in Dettaï and Lecointre (2005). It is contradicted by studies using complete mitochondrial sequence data (Miya et al., 2001, 2003, 2005, 2007) on a single point: the Lampridiformes are attracted to a non-acanthomorph group (either Myctophiformes or Ateleopodiformes). In Miya et al. (2007), RAG1 places Lampridiformes sister to the Acanthopterygii. Our large-scale clade P contains two orders of the former paracanthopterygians (Percopsiformes and Gadiformes) and during the last ten years the polyphyly of the Paracanthopterygii has been demonstrated several times by independent teams and data: the Lophiiformes are members of clade N, the Gobiesociformes members of clade D and the Batrachoidiformes the sister-group of what we call here clade F (Miya et al., 2005).
- Basal Acanthomorpha: present results corroborate that clade P is the most basal among acanthomorphs sampled here and that ophidiiforms (cusk-eels) are the sister-group of non-P and non-beryciform acanthomorphs (as in Miya et al., 2003, 2005).

A number of groups are found in several trees however they are absent from Fig. 5 and not considered to be reliable. They can be used as working hypotheses.

- Clade U: *Pampus* (Stromateidae) sister-group of all other members of H in Figs. 2–4;
- Clade V: Carangimorpha (L) + Anabantiformes (F) found in Figs. 2–4;
- Extended N: clade N including Monodactylidae (fingerfishes), Lutjanidae (snappers), Leiognathidae (ponyfishes), Cepolidae (bandfishes), Labridae (wrasses), Scaridae (parrotfishes) and Moronidae, Centrarchidae, Elassomatidae, Callanthiidae (groppos), Priacanthiidae (bigeyes), Caesionidae (fusiliers), Scatophagidae (scats), Malacanthidae (tilefishes), Datnioididae

(tigerperches), Kyphosidae (sea chubs), Aplodactylidae (marblefishes), Cheilodactylidae (morwongs), Sparidae (porgies), Champsodontidae (crocodile toothfishes), clades X, G, M′ and R.

As discussed above, a clade can be considered reliable when it has been recovered on several independent datasets, and whenever possible by several teams independently. New clades are hypotheses of interrelationships that need to be tested through various sources of data by other teams before being accepted by the community. This is why new clades temporarily received letters (as in Chen et al., 2003; Kawahara et al., 2008; Dettaï and Lecointre, 2005; Dettaï and Lecointre, 2008) suggesting that they were working hypotheses. However, as letters differ from one study to another for the same clades, a need for stabilization emerges. Once the new clades are sufficiently corroborated, it becomes necessary to give them names, for convenience' sake. In the case of acanthomorphs, the new names were proposed by Johnson and Patterson (1993). Almost none of the molecular studies of large-scale acanthomorph interrelationships (Chen et al., 2000, 2003; Wiley et al., 2000; Miya et al., 2001, 2003; Dettaï and Lecointre, 2004, 2005, 2008; Smith and Wheeler, 2004, 2006) proposed new names. It is striking that, while many clades were recovered several times from independent genes and teams, they still remain unnamed. Table 4 proposes names for the clades that have been repeatedly recovered in the molecular phylogenies of acanthomorphs.

All the 311 (Nelson, 2006) acanthomorph families have not yet been included in a single study. However this is not an obstacle and recommendations for names can be made progressively as new families are included. Smith and Craig (2007) added new evidence and summarized results from different studies. They then proposed new and necessary delimitations for serranids, percoids, trachinoids, resurrected epinephelids and niphonids, and created the Moronoidei. We have a single minor point of disagreement with their propositions: they proposed to incorporate the Notothenioidei and the Percophidae into the new Notothenioidea. 'Notothenioidei' has the suborder termination; while 'Notothenioidea' has the super family termination: the second cannot contain the first. Therefore, the name Notothenioidea should be replaced by the name Notothenioidi. The status of our Notothenioidiformes with regard to Smith and Craig's Percoidei will be clarified once sequences of *Niphon*, *Acanthistius* and *Bembrops* will be accessible for the present four molecular markers.

4.2. Supertrees and reliability

In Li and Lecointre (2008), since all trees were built on the same set of taxa, the repetition indices could easily be mapped on the summary tree. Here, the MRP supertree plays the role of a summary tree and is obtained from several partially-overlapping third-level validity domains. Since the repetition indices that were used to weight the clades are only valid in their restricted validity domains, no repetition index is displayed on the supertree. MRP is known to have biases. Even if the bipartitions were weighted according to their repetition indices, the reliability of clades shown in the summary tree holds if the supertree method used is itself accurate. Moreover, our conclusions could be affected by some taxa with undetermined position because the method (supertree based on clades weighted according to Li and Lecointre's repetition index) does not seem to handle well taxa present in only one elementary dataset (e.g. as a result *Acanthistius*, *Plectropomus* and *Liopropoma* do not join serranids, *Aeoliscus* does not group with macrorhamphosids, *Centropomus* is not close to *Lates*, *Balistes* fails to join the Tetraodontiformes, *Pseudaphritis* fails to join notothenioids, *Encheliophis* is not close to *Echiodon*). The interpretation given to clades present in the 'total evidence' tree (Fig. 4) and not in Fig. 5—as a possible bias in the tree from the 'total evidence'—must therefore be taken with caution.

Acknowledgments

This work was supported by the 'Consortium National de Recherche en Génomique', and the 'Service de Systématique Moléculaire' of the Muséum National d'Histoire Naturelle (IFR 101). It is part of the agreement number 2005/67 between the Genoscope and the Muséum National d'Histoire Naturelle on the project 'Macrophylogeny of life' directed by Guillaume Lecointre. Part of this work was carried out by using the resources of the Computational Biology Service Unit from the Muséum National d'Histoire Naturelle (MNHN) which was partially funded by Saint Gobain. Thanks to Damien Hinsinger for some of the new MLL sequences. Thanks to Bruno Chanet and Laure Corbari for help and advice. The name 'Stiassnyiformes' is proposed for clade Q, refering to the title of the paper of Stiassny (1993).

Figures were prepared using TikZ (http://sourceforge.net/projects/pgf/), TreeGraph (Müller and Müller, 2004), Inkscape (http://www.inkscape.org/) and Ipe (http://tclab.kaist.ac.kr/ipe/).

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