



ASSESSING METABOLIC CONSTRAINTS ON THE MAXIMUM BODY SIZE OF ACTINOPTERYGIANS: LOCOMOTION ENERGETICS OF *LEEDSICHTHYS PROBLEMATICUS* (ACTINOPTERYGII, PACHYCORMIFORMES)

by HUMBERTO G. FERRÓN^{1,*} , BORJA HOLGADO^{2,*} , JEFFREY J.
LISTON^{3,4,5,6}, CARLOS MARTÍNEZ-PÉREZ^{1,6} and HÉCTOR BOTELLA¹

¹Institut Cavanilles de Biodiversitat i Biologia Evolutiva, Universitat de València, C/Catedràtic José Beltrán Martínez 2, 46980, Paterna, Valencia Spain; humberto.ferron@uv.es, carlos.martinez-perez@uv.es, hector.botella@uv.es

²Laboratory of Systematics & Taphonomy of Fossil Vertebrates, Departamento de Geología e Paleontología, Museu Nacional/Universidade Federal do Rio de Janeiro (UFRJ), Quinta da Boa Vista, s/n, São Cristóvão, 20940-040, Rio de Janeiro, RJ Brazil; borja.holgado@mn.ufrj.br

³Bayerische Staatssammlung für Paläontologie und Geologie, Richard-Wagner-Straße 10, 80333, München, Germany; j.liston@lrz.uni-muenchen.de, leedsichthys@gmail.com

⁴National Museums Scotland, Chambers Street, Edinburgh, EH1 1JF, UK; j.liston@nms.ac.uk

⁵Institute of Biodiversity, Animal Health and Comparative Medicine, College of Medical, Veterinary and Life Sciences, University of Glasgow, Glasgow, UK; jeff.liston@glasgow.ac.uk

⁶School of Earth Sciences, University of Bristol, Bristol, BS8 1TQ, UK; glzjl@bristol.ac.uk, carlos.martinez-perez@bristol.ac.uk

*Corresponding authors

Typescript received 21 October 2017; accepted in revised form 5 April 2018

Abstract: Maximum sizes attained by living actinopterygians are much smaller than those reached by chondrichthyans. Several factors, including the high metabolic requirements of bony fishes, have been proposed as possible body-size constraints but no empirical approaches exist. Remarkably, fossil evidence has rarely been considered despite some extinct actinopterygians reaching sizes comparable to those of the largest living sharks. Here, we have assessed the locomotion energetics of *Leedsichthys problematicus*, an extinct gigantic suspension-feeder and the largest actinopterygian ever known, shedding light on the metabolic limits of body size in actinopterygians and the possible underlying factors that drove the gigantism in pachycormiforms. Phylogenetic generalized least squares analyses and power performance curves established in living fishes were used to infer the metabolic budget and locomotion cost of *L. problematicus* in a wide range of scenarios. Our approach predicts that specimens

weighing up to 44.9 tonnes would have been energetically viable and suggests that similar body sizes could also be possible among living taxa, discarding metabolic factors as likely body size constraints in actinopterygians. Other aspects, such as the high degree of endoskeletal ossification, oviparity, indirect development or the establishment of other large suspension-feeders, could have hindered the evolution of gigantism among post-Mesozoic ray-finned fish groups. From this perspective, the evolution of anatomical innovations that allowed the transition towards a suspension-feeding lifestyle in medium-sized pachycormiforms and the emergence of ecological opportunity during the Mesozoic are proposed as the most likely factors for promoting the acquisition of gigantism in this successful lineage of actinopterygians.

Key words: metabolic constraints, body size, gigantism, actinopterygians, Pachycormiformes, *Leedsichthys problematicus*.

Giant animals have intrigued both popular culture and the scientific community for many centuries. The largest living vertebrates occur in the oceans as massive suspension-feeders, reaching more than 50 tonnes in weight (Ferrón *et al.* 2017), closely linked to areas of high planktonic productivity (Vermeij 2016 and references therein). Although this ecological role has exclusively been occupied by mysticete cetaceans and some chondrichthyans

throughout the Cenozoic, the first unequivocal gigantic suspension-feeders were representatives of a Mesozoic group of actinopterygians called pachycormiforms (Friedman *et al.* 2010). The largest representative by far of this extinct lineage is *Leedsichthys problematicus*, a Middle–Late Jurassic species known from the Callovian of England (Peterborough, Christian Malford), France (Normandy), northern Germany (Wiehengebirge), the Oxfordian of

Chile (east of Antofagasta) and the Kimmeridgian of France (Cap de la Hève) (Liston 2010), being considerably larger than the contemporary and subsequent Cretaceous suspension-feeding pachycormiforms (Liston 2008, 2013; Schumacher *et al.* 2016). *Leedsichthys* is preserved in the fossil record as isolated, poorly ossified (Liston 2004) and fragmentary skeletal remains, leading to its frequent misidentification as organisms other than fish (Liston 2010; Liston & Gendry 2015), and most frequently as a stegosaurian dinosaur (Liston 2016). The most complete specimen ever recorded still represents only a partial individual (Liston 2006), but some remains have served to indicate the large size of this taxon with great clarity (Liston & Noè 2004; Liston 2008). As such, body size estimates of *L. problematicus* have been based on allometric relationships established in the most closely related large bony fish which is likely to have the most comparable form: the pachycormiform *Saurostomus esocinus* (Liston 2007; Liston *et al.* 2013). The dimensions of preopercular remains found with a ventral gill basket (Liston 2008) suggest that *L. problematicus* reached body lengths of up to 16.5 m. (Liston *et al.* 2013), which would make it the largest bony fish known among both living and fossil species, and is approximately the size of the largest chondrichthyan.

Recently, some metabolic aspects have been proposed as constraining factors of both body size and activity level in animals. Makarieva *et al.* (2006) suggested that the physiological viability of all organisms is limited by a minimum critical value of mass-specific metabolic rate. Thus, since mass-specific metabolic rate decreases as the size of organisms increases, larger sizes are not physiologically viable once this limit has been reached. Similarly, this implies that cost of locomotion at certain swimming speeds or highly energetic activities is not affordable over particular size thresholds (Ferrón *et al.* 2017). Ferrón (2017) established a methodology for assessing the energetic budget and cost of locomotion in extinct aquatic vertebrates, allowing the determination of the range of sizes within which a given activity (e.g. active predation or suspension-feeding) can be sustained on a long-term basis. Based on this idea, we here establish a similar framework to evaluate the swimming energetics of *L. problematicus*, shedding light on the metabolic limits of body size in actinopterygians, and discuss the possible underlying factors that drove the gigantism and success of Mesozoic suspension feeding pachycormiform fishes.

MATERIAL AND METHOD

The swimming energetics of *Leedsichthys problematicus* were evaluated assuming different environmental and phylogenetic scenarios by comparing estimates of its energy budget (assessed by its routine metabolic rate)

with independent inferences of its locomotion energy requirements (i.e. net cost of swimming).

Routine metabolic rate (RMR), defined as the mean metabolic rate measured in an animal performing random physical activity over a given period (Dowd 2003), can be considered in a broad sense to be equivalent to its energetic budget (Willmer *et al.* 2009; Clarke 2013). The scaling of RMR with mass has been established in living ectothermic fishes by means of phylogenetic generalized least squares (PGLS) analysis and is used here to infer RMR of *L. problematicus*. PGLS is a phylogenetic regression method in which the covariance among specimens as a result of their shared evolutionary history (i.e. phylogeny) is incorporated in the regression error term, thus being accounted for during the analysis (see Symonds & Blomberg 2014 for a general introduction to PGLS analysis). Records of RMR and body mass have been compiled for more than 100 fish species from Froese & Pauly (2017) and Ferrón (2017) (data in Ferrón *et al.* 2018). A super-tree containing all the considered species was constructed based on the phylogenies provided by Betancur *et al.* (2013) and Vélez-Zuazo & Agnarsson (2011) using Mesquite software version 3.2 (Maddison & Maddison 2017). RMR data were temperature adjusted to 20, 25 and 30°C with a Q_{10} of 2 (factor by which the oxygen consumption increases for every 10° rise in the temperature), covering the presumed range of temperatures inhabited by *L. problematicus* (Anderson *et al.* 1994; Jenkyns *et al.* 2012). RMR and body mass data were log-transformed and PGLS analysis was conducted, at each temperature, by means of R software version 3.4.0 (R Core Team 2017) using the ape package version 4.1 (Paradis *et al.* 2004) and the caper package version 0.5.2 (Orme 2013) with the maximum likelihood transformation of branch lengths optimized for the data ('lambda = ML'). Estimated values of lambda were used and kappa and delta were fixed at 1. *L. problematicus* body mass was calculated following Webb (mass = 0.01 L³; Webb 1975, following Bainbridge 1961) using the previously-derived estimate of *L. problematicus* maximum body length (i.e. 16.5 m according to Liston *et al.* 2013; this was also used as the basis for depicting the body mass of *Leedsichthys* in Ferrón 2017 and Ferrón *et al.* 2017) and cross-checked with a scale model as per Motani (2001) (see Liston 2007 for full description). RMR of *L. problematicus* was then inferred from its body mass in all three scenarios by interpolation in the established models.

Net cost of swimming (NCS) of *L. problematicus* was calculated from power-performance curves of living actinopterygians as the difference between the total metabolic rate (TMR, oxygen consumption at a particular swimming speed) and the standard metabolic rate (SMR, oxygen consumption at resting). We selected power performance curves relating the swimming speed and the

oxygen consumption of both living non-teleostean (*Acipenser naccarii*) and teleostean fishes (*Oncorhynchus kisutch* and *Gadus morhua*) in different environments (marine, brackish and freshwater). In the wake of recent analysis showing deep flaws in the previous placement of *L. problematicus* as a stem teleost, the taxon is conservatively regarded as Neopterygii *incertae sedis* (Arratia & Schultze 2013; Schultze & Arratia 2013). However, for the purposes of physiological comparisons, a teleostean affinity (Arratia 2004) under marine conditions (Liston 2010) would be the most appropriate combination of taxonomic approximation and environmental parameters to employ for inferences on *L. problematicus*. The mathematical formulation of the approach is as follows:

$$\text{MO}_{2A.naccariiFW} = 187 \times 2.72^{0.308U}$$

(Power performance equation from McKenzie *et al.* 2001a) from which it is deduced that

$$\text{TMR}_{(U>0)A.naccariiFW} = 187 \times 2.72^{0.308U}$$

$$\text{SMR}_{(U=0)A.naccariiFW} = 187$$

$$\text{NCS}_{A.naccariiFW} = \text{TMR} - \text{SMR} = 187 \times 2.72^{0.308U} - 187$$

$$\text{MO}_{2A.naccariiBW} = 303 \times 2.72^{0.247U}$$

(Power performance equation from McKenzie *et al.* 2001a) from which it is deduced that

$$\text{TMR}_{(U>0)A.naccariiBW} = 303 \times 2.72^{0.247U}$$

$$\text{SMR}_{(U=0)A.naccariiBW} = 303$$

$$\text{NCS}_{A.naccariiBW} = \text{TMR} - \text{SMR} = 303 \times 2.72^{0.247U} - 303$$

$$\text{MO}_{2A.naccariiMW} = 254 \times 2.72^{0.301U}$$

(Power performance equation from McKenzie *et al.* 2001b) from which it is deduced that

$$\text{TMR}_{(U>0)A.naccariiMW} = 254 \times 2.72^{0.301U}$$

$$\text{SMR}_{(U=0)A.naccariiMW} = 254$$

$$\text{NCS}_{A.naccariiMW} = \text{TMR} - \text{SMR} = 254 \times 2.72^{0.301U} - 254$$

$$\text{MO}_{2O.kisutchFW} = 60 \times (2.37 + 0.25 \times 2.72^{1.93U})$$

(Power performance equation from Lee *et al.* 2003) from which it is deduced that

$$\text{TMR}_{(U>0)O.kisutchFW} = 60 \times (2.37 + 0.25 \times 2.72^{1.93U})$$

$$\text{SMR}_{(U=0)O.kisutchFW} = 157.2$$

$$\text{NCS}_{O.kisutchFW} = \text{TMR} - \text{SMR}$$

$$= 60 \times (2.37 + 0.25 \times 2.72^{1.93U}) - 157.2$$

$$\text{MO}_{2G.morhuaMW} = 10^{2.122+0.21U}$$

(Power performance equation from Soofiani & Priede 1985) from which it is deduced that

$$\text{TMR}_{(U>0)G.morhuaMW} = 10^{2.122+0.21U}$$

$$\text{SMR}_{(U=0)G.morhuaMW} = 1$$

$$\text{NCS}_{G.morhuaMW} = \text{TMR} - \text{SMR} = 10^{2.122+0.21U} - 1$$

where MO_2 is oxygen consumption, TMR is total metabolic rate, SMR is standard metabolic rate and NCS is net cost of swimming, all them in milligrams of oxygen per kilogram and hour ($\text{mgO}_2/\text{kg/h}$); U is relative swimming speed in body lengths per second (BL/s); FW, BW and MW refer to fresh, brackish and marine water conditions respectively.

NCS was inferred in each case at three different swimming speeds: 0.05 body lengths per second (as a conservative speed based on records of similar-sized living suspension feeding fishes; see Ferrón 2017, table S4), 0.14 body lengths per second (as the optimal suspension-feeding speed for a 16.5 m fish according to Weihs & Webb's 1983 model) and 0.30 body lengths per second (as the optimal cruising speed for a 16.5 m fish according to Peters' 1983 approach).

RESULTS

The phylogenetic generalized least squares (PGLS) analysis detected a highly significant correlation between RMR and body mass in all three considered temperature scenarios (i.e. 20, 25 and 30°C; p -value = 2.2×10^{-16} , $R^2 = 0.85$) (Fig. 1). We estimated a maximum total body mass of 44.9 tonnes for *Leedsichthys problematicus*, which provided RMR estimates of 101, 143 and 202 mg of oxygen per kilogram and hour ($\text{mgO}_2/\text{kg/h}$) at 20, 25 and 30°C respectively after extrapolation in the PGLS models (Fig. 2).

L. problematicus NCS estimates varied depending on the swimming speed, phylogenetic and environmental scenario but in no case exceeded the RMR estimates (Fig. 2). As expected, NCS estimates were higher when considering faster swimming speeds. The teleostean scenario entailed slightly lower NCS estimates than the non-teleostean one when comparing similar conditions of salinity and swimming speeds. Finally, NCS estimates were also higher when considering environments with higher salinity concentrations both in the teleostean and non-teleostean scenarios.

DISCUSSION

Maximum body sizes of living actinopterygians and chondrichthyans differ considerably. The heaviest extant ray-finned fish (*Mola mola* with up to 2.3 tonnes; Pope *et al.*

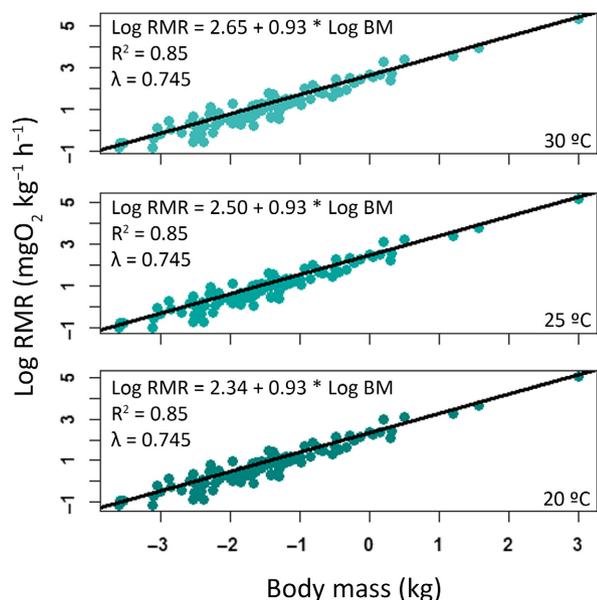


FIG. 1. Phylogenetic generalized least squares analyses between routine metabolic rate (RMR) and body mass (BM) of living fishes at three different temperature scenarios (20, 25 and 30°C). RMR is expressed as milligrams of oxygen per kilogram and hour ($\text{mgO}_2/\text{kg}/\text{h}$) and body mass as kilograms (kg). Colour online.

2010) is one order of magnitude smaller than the largest cartilaginous fish (*Rhincodon typus* with up to 34 tonnes; Froese & Pauly 2017) and much smaller than many other sharks (see Ebert *et al.* 2013). Among zoologists, such size discrepancy is a matter of debate and various different constraints have been proposed for explaining this phenomenon (see a detailed review in Freedman & Noakes 2002). Remarkably, evidence coming from fossil groups has rarely been considered, despite the fact that some key taxa, such as large pachycormiforms, could provide important clues in this regard. In fact, here we estimate that the largest specimens of *Leedsichthys problematicus* could have weighed up to 44.9 tonnes, reaching a considerably larger body mass than the heaviest known chondrichthyans and making this extinct fish a target taxon for exploring the limiting factors of body size in actinopterygians.

Is the maximum body size of actinopterygians constrained by energetics?

Metabolic rate acts as a constraining factor on activity, feeding strategy and body size in living organisms (Makarieva *et al.* 2005a, b, 2006; Ferrón *et al.* 2017). The high metabolic demand of bony fishes has sometimes been proposed as a possible explanation of the well-known differences in the maximum body size of living

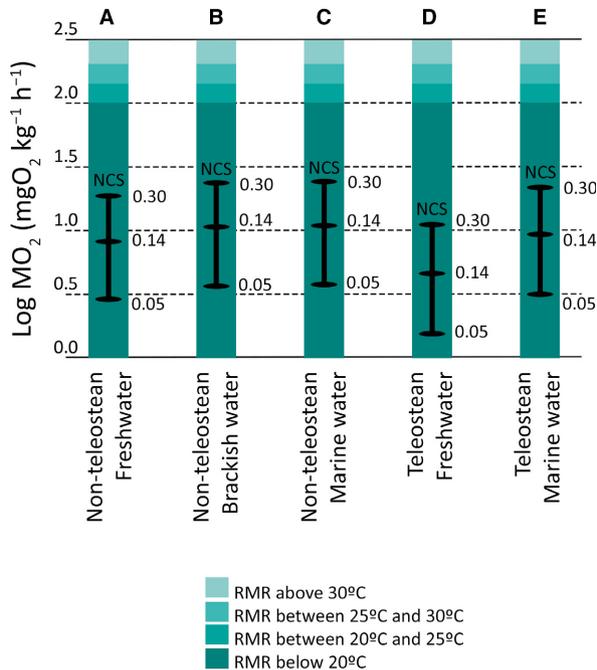


FIG. 2. Comparison of routine metabolic rate (RMR) and net cost of swimming (NCS) (at 0.05, 0.14 and 0.30 body lengths per second) of a 44.9 tonne *Leedsichthys problematicus*, considering different environmental and phylogenetic scenarios. Graded shading represents RMR at different water temperatures. NCS calculated from power–performance curves of: A–C, *Acipenser naccarii* from McKenzie *et al.* (2001a, b); D, *Oncorhynchus kisutch* from Lee *et al.* (2003); E, *Gadus morhua* from Soofiani & Priede (1985). NCS is constant in all temperature scenarios (see text). Oxygen consumption (MO_2) is expressed as milligrams of oxygen per kilogram and hour ($\text{mgO}_2/\text{kg}/\text{h}$). Colour online.

chondrichthyans and actinopterygians (Freedman & Noakes 2002 and references therein). Recently, Ferrón (2017) established a methodology for assessing the locomotion energetics and metabolic constraints on the body size of sharks by comparing estimates of their energetic budget (\approx routine metabolic rate (RMR)) and locomotion energetic requirements (\approx net cost of swimming (NCS)). The predictive power of such a procedure was tested in 17 living species by contrasting inferences derived from this approach with real body size, metabolic and physiological measurements, demonstrating a reliable applicability for assessing energetics in extinct taxa. Here, based on that work, we have developed a parallel methodology from living fish data in order to explore the locomotion energetics of *L. problematicus*, assessing the body size metabolic limits of ray-finned fishes. The phylogenetic generalized least squares (PGLS) analyses support the relationship between RMR and body mass as being well-founded (p -value = 2.2×10^{-16} ; $R^2 = 0.85$) (Fig. 1) and that the model can be reliably used for predicting the

RMR (and the energetic budget) of extinct fishes. Power performance curves calculated in small living fishes (relating the oxygen consumption and swimming speed) have been revealed as suitable models for predicting the cost of locomotion of much larger free-swimming species (Sundström & Gruber 1998; Semmens *et al.* 2013) and extinct taxa (Ferrón 2017). More specifically, the use of net cost of swimming (NCS) as an approximation of the energy expenditure of thrust generation during swimming is especially useful when considering different environmental scenarios, since this parameter seems to be independent of the water temperature (William & Beamish 1990; Claireaux *et al.* 2006; Ohlberger *et al.* 2007) (see Ferrón 2017 for further discussion). Here, power performance curves of living actinopterygians have been used for the first time to assess the NCS in an extinct taxon. According to our approach, the energetic budget of *L. problematicus* (i.e. RMR) considerably exceeded its locomotion cost (i.e. NCS) in a wide range of scenarios, considering this taxon as a teleostean and non-teleostean actinopterygian swimming at different speeds, water temperatures and salinities (Fig. 2). Given that the costs derived from locomotion constitute the main amount of the energetic expenditure in fishes (Priede 1985), these results suggest that metabolic aspects cannot be regarded as a major constraining factor of the size of living actinopterygians and that individuals with similar (or even bigger) body masses to that of *L. problematicus* could be also potentially viable in energetic terms among extant groups. Therefore, other aspects should be discussed as potential limiting factors of maximum body size in living ray-finned fishes.

Possible constraints on the maximum body size of actinopterygians

Many factors have been regarded as potential size constraints on bony fishes (see Freedman & Noakes 2002 and references therein). However, only a few of them seem to be better supported on existing evidence and deserve special attention in future studies. Life-history and ontogenetic traits such as the existence of oviparity and indirect development have been proposed as the most likely limiting factors of the maximum size of teleosts. The small size of the larvae/juveniles imposed by the production of tiny eggs as well as the high energetic expenditure derived from the metamorphosis are indeed determinant factors of the final adult size in fishes (Freedman & Noakes 2002). In fact, most of the biggest aquatic animals, including an important number of sharks, coelacanths, extinct marine reptiles and marine mammals, belong to groups that have direct development of relatively large offspring (Wourms *et al.* 1991; Folkens & Randall 2002; Motani 2009; Ebert *et al.* 2013). Besides that, endoskeletal

ossification (particularly important in teleostean fishes) could also constitute a constraining element in this sense, given that bone takes more time and energy to create than cartilage (Gilbert 2000), and a high bone mass can considerably increase the energy required for acceleration and deceleration in water (Biewener 1983). Freedman & Noakes (2002) argued that this might not represent a real limitation for the maximum size of aquatic animals as there are numerous examples of giant cetaceans and extinct marine reptiles with calcified skeletons. However, these examples comprise only endo- or mesotherm taxa, which have an accelerated metabolism and a wider metabolic budget than ectotherms (Careau *et al.* 2014), entailing faster growth rates and a greater capacity to deal with higher metabolic demands. In fact, the largest ectothermic fishes belong to groups with poorly-calcified cartilaginous endoskeletons (such as chondrichthyans, Nelson *et al.* 2016) or have secondarily acquired this condition from bony ancestors (e.g. acipenseriforms, Nelson *et al.* 2016; or the teleostean *Mola mola*, Pope *et al.* 2010). Therefore, it is likely that the energetic investment of developing and swimming with a well-ossified endoskeleton constitutes an important trade-off for ectothermic aquatic vertebrates. Finally, the evolution of several lineages of giant vertebrates follows similar trajectories (i.e. cetaceans, pachycormiforms and placoderms) where the acquisition of the largest body sizes occurs after the apparent adaptation to suspension feeding (Friedman 2012). Therefore, ecological scenarios that prevent the occupation of such ecospace may also hinder the evolution of gigantic body sizes. In this sense, well-established lineages of Cenozoic suspension feeding cetaceans and chondrichthyans could have competitively excluded actinopterygians from exploring similar lifestyles.

The rise of gigantic suspension-feeding pachycormiforms

A subset of pachycormiforms successfully faced these limitations reaching the most gigantic sizes ever recorded in bony fishes. Despite the singularity of these taxa, the reasons that promoted the acquisition of such huge body sizes have been little discussed so far and remain unclear (see Liston 2007; Friedman 2012; Liston *et al.* 2013). This group of pachycormiforms sequentially acquired a number of anatomical innovations that facilitated, in medium-sized forms, the ecological shift from an ancestral macropredatory lifestyle to a suspension-feeding strategy (Fig. 3). Modifications in the mandibular aspect ratio, the loss of dentition, and the acquisition of well-developed gill rakers played a crucial role in this evolutionary transition (Liston 2013; Friedman 2012 and references therein). The attainment of gigantic sizes occurred after the ecological shift to suspension-feeding was completed, mirroring

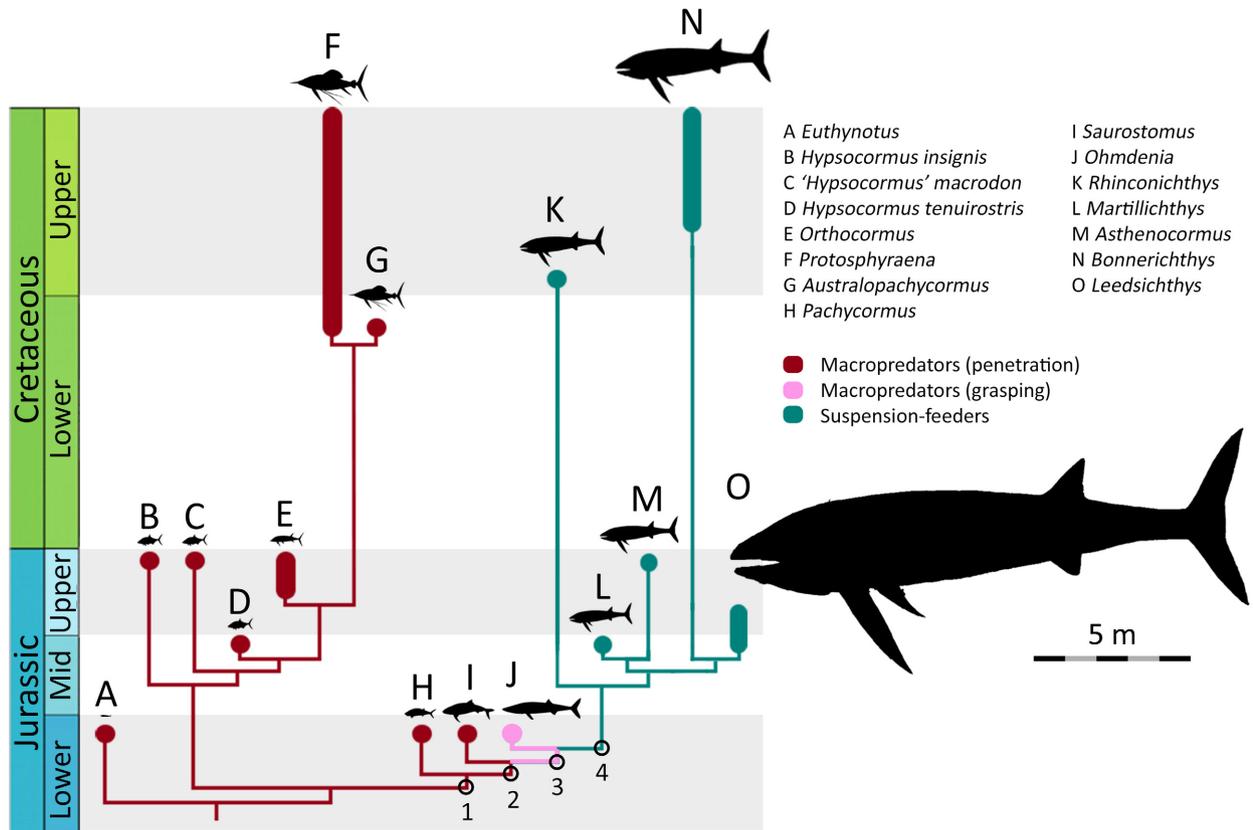


FIG. 3. Main anatomical innovations and body size dynamics along the evolutionary ecological shift from macropredation to suspension feeding strategy in pachycormiforms. 1, unossified sections in the vertebral column; 2, unossified vertebral column and loss of some dermal skull elements; 3, loss of scales and pleural ribs, and modifications in mandibular aspect ratio; 4, well-developed gill rakers and loss of dentition. Figure modified from Friedman (2012) following phylogenetic relationships proposed by Schumacher *et al.* (2016). Colour online.

the patterns followed by most other groups of gigantic aquatic vertebrates (Friedman 2012). Interestingly, such parallelism may be satisfactorily explained from a metabolic perspective, considering that mass-specific metabolic rate decreases with increasing body mass and, as a consequence, gigantic sizes are only energetically viable with the previous acquisition of modes of life that entail low energetic requirements (Ferrón *et al.* 2017). In fact, the reduction of the dermoskeleton and bone mass with increasing adult size is also a phyletic trend across the pachycormiforms that could be interpreted as an adaptation for minimizing energetic expenditure in the biggest species (Liston 2007; Liston *et al.* 2013) (Fig. 3). On the other hand, high local primary productivity of some areas (Liston 2007 and references therein) and the absence of other big suspension feeding taxa during most of the Mesozoic (Friedman *et al.* 2010) could have offered the pachycormiforms an ecological opportunity for filling this ecospace. Unfortunately, other aspects that seem to be relevant in the evolution of gigantic sizes of living taxa, such as the reproductive strategy (Friedman & Noakes 2002), remain speculative in pachycormiforms because of

the lack of fossil evidence (Liston 2007). In any case, the evolution of viviparity with direct development in this group could be a likely scenario given the large sizes reached by its largest representatives, especially if we take into account the fact that this reproductive strategy has repeatedly evolved throughout the evolutionary history of bony fishes (Blackburn 2015). Therefore, pending new fossil evidence, we propose that the ecological shift to a suspension feeding lifestyle in medium-sized forms, and the emergence of ecological opportunity, were the primary factors that permitted pachycormiforms to explore new zones within the potential metabolic spectrum of bony fishes, and the acquisition of gigantic sizes, triggering in conjunction the rise of this successful lineage of gigantic suspension feeders.

Author contributions. HGF and BH contributed equally to this work. JIL contributed data and discussion on pachycormiforms.

Acknowledgements. We would like to thank Dr Guilherme R. S. Muricy (Museu Nacional/Universidade Federal do Rio de Janeiro) for his assistance on discussions and Dr Ximena Véllez-

Zuazo (University of Puerto Rico) for making available to us the phylogeny (NEXUS) files of Vélez-Zuazo & Agnarsson (2011). We acknowledge the comments of Dr Lionel Cavin (Editor), Dr Sally Thomas (Editor), Dr Hugo Martín Abad (referee) and an anonymous reviewer who considerably improved the final manuscript. This work was supported by the Spanish Ministry of Economy and Competitiveness (Research Project CGL2014-52662-P); and the Generalitat Valenciana (Research Project GV/2016/102). Humberto G. Ferrón is a recipient of a FPU Fellowship from the Spanish Ministry of Education, Culture and Sport (Grant FPU13/02660) and Borja Holgado is a recipient of a PhD fellowship (140789/2016-2) of the Brazilian Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq).

DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.mt78r>

Editor. Lionel Cavin

REFERENCES

- ANDERSON, T. F., POPP, B. N., WILLIAMS, A. C., HO, L.-Z. and HUDSON, J. D. 1994. The stable isotopic records of fossils from the Peterborough Member, Oxford Clay Formation (Jurassic), UK: palaeoenvironmental implications. *Journal of the Geological Society*, **151**, 125–138.
- ARRATIA, G. 2004. Mesozoic halecostomes and the early radiation of teleosts. 279–315. In ARRATIA, G. and TINTORI, A. (eds). *Mesozoic fishes 3. Systematics, paleoenvironments and biodiversity*. Friedrich Pfeil, München, 649 pp.
- and SCHULTZE, H.-P. 2013. Outstanding features of a new Late Jurassic pachycormiform fish from the Kimmeridgian of Brunn, Germany and comments on current understanding of pachycormiforms. 87–120. In ARRATIA, G., SCHULTZE, H.-P. and WILSON, M. V. H. (eds). *Mesozoic fishes 5. Global diversity and evolution*. Friedrich Pfeil, München, 560 pp.
- BAINBRIDGE, R. 1961. Problems of fish locomotion. 13–32. In HARRIS, J. E. (ed.) *Vertebrate locomotion. Vol. 5*. Zoological Society of London, London, 132 pp.
- BETANCUR, R., BROUGHTON, R. E., WILEY, E. O., CARPENTER, K., LÓPEZ, J. A., LI, C., HOLCROFT, N. I., ARCILA, D., SANCIANGCO, M., CURETON, J. C. II, ZHANG, F., BUSER, T., CAMPBELL, M. A., BALLESTEROS, J. A., ROA-VARON, A., WILLIS, S., BORDEN, W. C., ROWLEY, T., RENEAU, P. C., HOUGH, D. J., LU, G., GRANDE, T., ARRATIA, G. and ORTÍ, G. 2013. The tree of life and a new classification of bony fishes. *PLOS Currents*, **5**, Edition 1. <https://doi.org/10.1371/currents.tol.53ba26640df0ccaee75bb165c8c26288>
- BIEWENER, A. A. 1983. Locomotory stresses in the limb bones of two small mammals: the ground squirrel and chipmunk. *Journal of Experimental Biology*, **103**, 131–154.
- BLACKBURN, D. G. 2015. Evolution of vertebrate viviparity and specializations for fetal nutrition: a quantitative and qualitative analysis. *Journal of Morphology*, **276**, 961–990.
- CAREAU, V., KILLEN, S. S. and METCALFE, N. B. 2014. Adding fuel to the “fire of life”: energy budgets across levels of variation in ectotherms and endotherms. 219–233. In MARTIN, L. B., GHALAMBOR, C. K. and WOODS, H. A. (eds). *Integrative organismal biology*. Wiley-Blackwell, 344 pp.
- CLAIREAUX, G., COUTURIER, C. and GROISON, A.-L. 2006. Effect of temperature on maximum swimming speed and cost of transport in juvenile European sea bass (*Dicentrarchus labrax*). *Journal of Experimental Biology*, **209**, 3420–3428.
- CLARKE, A. 2013. Dinosaur energetics: setting the bounds on feasible physiologies and ecologies. *The American Naturalist*, **182**, 283–297.
- DOWD, W. W. 2003. Metabolic rates and bioenergetics of juvenile sandbar sharks (*Carcharhinus plumbeus*). Unpublished MSc thesis. The College of William & Mary, Williamsburg, VA, 152 pp.
- EBERT, D. A., FOWLER, S. L. and COMPAGNO, L. J. 2013. *Sharks of the world: a fully illustrated guide*. Wild Nature Press, Plymouth, 528 pp.
- FERRÓN, H. G. 2017. Regional endothermy as a trigger for gigantism in some extinct macropredatory sharks. *PLOS One*, **12**, e0185185.
- MARTÍNEZ-PÉREZ, C. and BOTELLA, H. 2017. The evolution of gigantism in active marine predators. *Historical Biology*, **30**, 1–5.
- HOLGADO, B., LISTON, J. J., MARTÍNEZ-PÉREZ, C. and BOTELLA, H. 2018. Data from: Assessing metabolic constraints on the maximum body size of actinopterygians: locomotion energetics of *Leedsichthys problematicus* (Actinopterygii: Pachycormiformes). *Dryad Digital Repository*. <https://doi.org/10.5061/dryad.mt78r>
- FOLKENS, P. A. R. and RANDALL, R. 2002. *Guide to marine mammals of the world*. National Audubon Society, New York, 527 pp.
- FREEDMAN, J. A. and NOAKES, D. L. 2002. Why are there no really big bony fishes? A point-of-view on maximum body size in teleosts and elasmobranchs. *Reviews in Fish Biology & Fisheries*, **12**, 403–416.
- FRIEDMAN, M. 2012. Parallel evolutionary trajectories underlie the origin of giant suspension-feeding whales and bony fishes. *Proceedings of the Royal Society B*, **279**, 944–951.
- SHIMADA, K., MARTIN, L. D., EVERHART, M. J., LISTON, J., MALTESE, A. and TRIEBOLD, M. 2010. 100-million-year dynasty of giant planktivorous bony fishes in the Mesozoic seas. *Science*, **327**, 990–993.
- FROESE, R. and PAULY, D. 2017. FishBase v. 02/2018. www.fishbase.org [accessed October 2017]
- GILBERT, S. F. 2000. Osteogenesis: the development of bones. 507–510. In GILBERT, S. F. (ed.) *Developmental biology*, 6th edn, Sinauer Associates, Sunderland, MA, 881 pp.
- JENKYNS, H. C., SCHOUTEN-HUIBERS, L., SCHOUTEN, S. and DAMSTÉ, J. S. 2012. Warm Middle Jurassic–Early Cretaceous high-latitude sea-surface temperatures from the Southern Ocean. *Climate of the Past*, **8**, 215–226.
- LEE, C. G., FARRELL, A. P., LOTTO, A., MACNUTT, M. J., HINCH, S. G. and HEALEY, M. C. 2003. The effect

- of temperature on swimming performance and oxygen consumption in adult sockeye (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon stocks. *Journal of Experimental Biology*, **206**, 3239–3251.
- LISTON, J. J. 2004. An overview of the pachycormiform *Leedsichthys*. 379–390. In ARRATIA, G. and TINTORI, A. (eds). *Mesozoic fishes 3. Systematics, paleoenvironments and biodiversity*. Friedrich Pfeil, München, 649 pp.
- 2006. From Glasgow to the Star Pit and Stuttgart: a short journey around the world's longest fish. *The Glasgow Naturalist*, **24**, 59–71.
- 2007. A fish fit for Ozymandias? The ecology, growth and osteology of *Leedsichthys* (Pachycormidae, Actinopterygii). Unpublished PhD thesis. University of Glasgow, 464 pp.
- 2008. A review of the characters of the edentulous pachycormiforms *Leedsichthys*, *Asthenocormus* and *Martillichthys* nov. gen. 181–198. In ARRATIA, G., SCHULTZE, H.-P. and WILSON, M. V. H. (eds). *Mesozoic fishes 4. Homology and phylogeny*. Friedrich Pfeil, München, 502 pp.
- 2010. The occurrence of the Middle Jurassic pachycormid fish *Leedsichthys*. *Oryctos*, **9**, 1–36.
- 2013. The plasticity of gill raker characteristics in suspension feeders: implications for Pachycormiformes. 121–143. In ARRATIA, G., SCHULTZE, H.-P. and WILSON, M. V. H. (eds). *Mesozoic fishes 5. Global diversity and evolution*. Friedrich Pfeil, München, 560 pp.
- 2016. *Leedsichthys problematicus*: Arthur Smith Woodward's 'most embarrassing enigma'. 235–259. In JOHANSON, Z., BARRETT, P. M., RICHTER, M. and SMITH, M. (eds). *Arthur Smith Woodward: his life and influence on modern vertebrate palaeontology*. Geological Society Special Publication, **430**, 362 pp.
- and GENDRY, D. 2015. Le Python de Caen, les algues géantes d'Amblie, et autres specimens perdus de *Leedsichthys* d'Alexandre Bourienne, Jules Morière, Eugène Eudes-Deslongchamps et Alexandre Bigot. *L'Écho des Falaises*, **19**, 17–33.
- and NOË, L. F. 2004. The tail of the Jurassic fish *Leedsichthys problematicus* (Osteichthyes: Actinopterygii) collected by Alfred Nicholson Leeds - an example of the importance of historical records in palaeontology. *Archives of Natural History*, **31**, 236–252.
- NEWBREY, M., CHALLANDS, T. and ADAMS, C. 2013. Growth, age and size of the Jurassic pachycormid *Leedsichthys problematicus* (Osteichthyes: Actinopterygii). 145–175. In ARRATIA, G., SCHULTZE, H.-P. and WILSON, M. V. H. (eds). *Mesozoic fishes 5. Global diversity and evolution*. Friedrich Pfeil, München, 560 pp.
- MADDISON, W. P. and MADDISON, D. R. 2017. *Mesquite: a modular system for evolutionary analysis*. v. 3.2. <http://mesquiteproject.org>
- MAKARIEVA, A. M., GORSHKOV, V. G. and LI, B.-L. 2005a. Temperature-associated upper limits to body size in terrestrial poikilotherms. *Oikos*, **111**, 425–436.
- — — 2005b. Gigantism temperature and metabolic rate in terrestrial poikilotherms. *Proceedings of the Royal Society B*, **272**, 2325–2328.
- — — and CHOWN S. L. 2006. Size-and temperature-independence of minimum life-supporting metabolic rates. *Functional Ecology*, **20**, 83–96.
- McKENZIE, D. J., CATALDI, E., ROMANO, P., OWEN, S. F., TAYLOR, E. W. and BRONZI, P. 2001a. Effects of acclimation to brackish water on the growth, respiratory metabolism, and swimming performance of young-of-the-year Adriatic sturgeon (*Acipenser naccarii*). *Canadian Journal of Fisheries & Aquatic Sciences*, **58**, 1104–1112.
- — — TAYLOR, E. W., CATAUDELLA, S. and BRONZI, P. 2001b. Effects of acclimation to brackish water on tolerance of salinity challenge by young-of-the-year Adriatic sturgeon (*Acipenser naccarii*). *Canadian Journal of Fisheries & Aquatic Sciences*, **58**, 1113–1121.
- MOTANI, R. 2001. Estimating body mass from silhouettes: testing the assumption of elliptical body cross-sections. *Paleobiology*, **27**, 735–750.
- 2009. The evolution of marine reptiles. *Evolution: Education & Outreach*, **2**, 224.
- NELSON, J. S., GRANDE, T. C. and WILSON, M. V. 2016. *Fishes of the World*, 5th edn. John Wiley & Sons, 752 pp.
- OHLBERGER, J., STAAKS, G. and HÖLKER, F. 2007. Effects of temperature, swimming speed and body mass on standard and active metabolic rate in vendace (*Coregonus albula*). *Journal of Comparative Physiology B*, **177**, 905–916.
- ORME, D. 2013. caper: comparative analysis of phylogenetics and evolution in R. v. 0.5.2. <https://cran.r-project.org/web/packages/caper/index.html>
- PARADIS, E., CLAUDE, J. and STRIMMER, K. 2004. APE: Analyses of Phylogenetics and Evolution in R language. *Bioinformatics*, **20**, 289–290.
- PETERS, R. H. 1983. *The ecological implications of body size*. Cambridge University Press, 329 pp.
- POPE, E. C., HAYS, G. C., THYS, T. M., DOYLE, T. K., SIMS, D. W., QUEIROZ, N., HOBSON, V. J., KUBICEK, L. and HOUGHTON, J. D. 2010. The biology and ecology of the ocean sunfish *Mola mola*: a review of current knowledge and future research perspectives. *Reviews in Fish Biology & Fisheries*, **20**, 471–487.
- PRIEDE, I. G. 1985. Metabolic scope in fishes. 33–64. In TYTLER, P. and CALOW, P. (eds). *Fish energetics: new perspectives*. Croom Helm, London, 349 pp.
- R CORE TEAM 2017. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna. <https://www.R-project.org>
- SCHULTZE, H.-P. and ARRATIA, G. 2013. The caudal skeleton of basal teleosts, its conventions, and some of its major evolutionary novelties in a temporal dimension. 187–246. In ARRATIA, G., SCHULTZE, H.-P. and WILSON, M. V. H. (eds). *Mesozoic fishes 5. Global diversity and evolution*. Friedrich Pfeil, München, 560 pp.
- SCHUMACHER, B. A., SHIMADA, K., LISTON, J. J. and MALTESE, A. E. 2016. Highly specialized suspension-feeding bony fish *Rhinconichthys* (Actinopterygii: Pachycormiformes) from the mid-Cretaceous of the United States, England, and Japan. *Cretaceous Research*, **61**, 71–85.
- SEMMENS, J. M., PAYNE, N. L., HUVENEERS, C., SIMS, D. W. and BRUCE, B. D. 2013. Feeding

- requirements of white sharks may be higher than originally thought. *Scientific Reports*, **3**, 1471.
- SOOFIANI, N. M. and PRIEDE, I. G. 1985. Aerobic metabolic scope and swimming performance in juvenile cod, *Gadus morhua* L. *Journal of Fish Biology*, **26**, 127–138.
- SUNDSTRÖM, L. F. and GRUBER, S. H. 1998. Using speed-sensing transmitters to construct a bioenergetics model for subadult lemon sharks, *Negaprion brevirostris* (Poey), in the field. *Hydrobiologia*, **371**, 241–247.
- SYMONDS, M. R. and BLOMBERG, S. P. 2014. A primer on phylogenetic generalised least squares. 105–130. In GARAMSZEGI, L. Z. (ed.) *Modern phylogenetic comparative methods and their application in evolutionary biology*. Springer, 552 pp.
- VÉLEZ-ZUAZO, X. and AGNARSSON, I. 2011. Shark tales: a molecular species-level phylogeny of sharks (Selachimorpha, Chondrichthyes). *Molecular Phylogenetics & Evolution*, **58**, 207–217.
- VERMEIJ, G. J. 2016. Gigantism and its implications for the history of life. *PLOS One*, **11**, e0146092.
- WEBB, P. W. 1975. Hydrodynamics and energetics of fish propulsion. *Bulletin of the Fisheries Research Board of Canada*, **190**, 1–158.
- WEIHS, D. and WEBB, P. W. 1983. Optimization of locomotion. 339–371. In WEBB, P. W. and WEIHS, D. (eds). *Fish biomechanics*. Prager, New York.
- WILLIAM, F. and BEAMISH, H. 1990. Swimming metabolism and temperature in juvenile walleye, *Stizostedion vitreum vitreum*. *Environmental Biology of Fishes*, **27**, 309–314.
- WILLMER, P., STONE, G. and JOHNSTON, I. 2009. *Environmental physiology of animals*. Blackwell Publishing, Carlton, Australia, 768 pp.
- WOURMS, J. P., ATZ, J. W. and STRIBLING, M. D. 1991. Viviparity and the maternal-embryonic relationship in the coelacanth *Latimeria chalumnae*. *Environmental Biology of Fishes*, **32**, 225–248.