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

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ABSTRACT

Maximum body sizes attained by living osteichthyans 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 have been conducted to assess this. Remarkably, the evidence coming from the fossil record has rarely been considered in studies dealing with this topic, despite some extinct actinopterygians reaching body 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 osteichthyan ever known, shedding light on the metabolic limits of body size in actinopterygians and the possible underlying factors that drove gigantism in Mesozoic pachycormiforms. For this, phylogenetic generalized least squares analyses and power performance curves established in living actinopterygians were used to infer the metabolic budget (≈routine metabolic rate, RMR) and locomotion costs (≈net costs of swimming, NCS) of *L. problematicus* in a wide range of phylogenetic and environmental scenarios. Our approach predicts that specimens with up to 44.9 tons would have been energetically viable and suggests that similar or even larger body sizes could also be possible among living taxa. As a consequence, we discard metabolic factors as likely body size constraints in actinopterygians, and suggest that other aspects, such as the high degree of endoskeletal ossification, oviparity, indirect development or the establishment of some sharks and cetaceans as 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, closely linked to areas of high planktonic productivity (Vermeij 2016). 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 pachycormids (Friedman *et al.* 2010). The largest representative of this extinct lineage is by far *Leedsichthys problematicus*, a Middle 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), dwarfing subsequent Cretaceous suspension-feeding pachycormids (SFPs) (Schumacher *et al*. 2016), as well as its two contemporary SFPs (Liston 2008; 2013). *Leedsichthys* preserves 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 and 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 and Noè 2004, Liston 2008). As such, body size estimates of *L. problematicus* have been based on allometric relationships established in other closely related bony fishes with comparable form (i.e., *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 osteichthyan known among both living and fossil species, and approximating the size of the largest chondrichthyan. Recently, some metabolic aspects have been proposed as constraining factors of the 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 ($mgO_2 \cdot h^{-1} \cdot kg^{-1}$). 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 costs of locomotion at certain swimming speeds or highly energetic activities are not affordable over particular size thresholds (Ferrón *et al.* 2017). Ferrón (2017) has recently established a methodology for assessing the energetic budget and the 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 pachycormid fishes.

MATERIAL AND METHODS

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 as equivalent to its energetic budget (Willmer *et al.* 2009; Clarke 2013). The scaling of

RMR with mass has been established in living ectothermic actinopterygians and used for inferring RMR of *L. problematicus*. For this, 94 records of RMR and body mass of actinopterygians have been compiled from FishBase (Froese and Pauly 2017) (Appendix S1). RMR data were temperature adjusted to 20ºC, 25ºC and 30ºC with a Q_{10} of 2, covering the presumed range of temperatures inhabited by this species (Anderson *et al.* 1994; Jenkyns *et al.* 2012). RMR and body mass data were log-transformed and a phylogenetic generalized least squares (PGLS) analysis was conducted, at each temperature, by means of R software version 3.4.0 (R Development Core Team 2017) using the ape package version 4.1 (Paradis *et al.* 2017) and the caper package version 0.5.2 (Orme 2013). The phylogenetic tree provided in Betancur *et al*. (2013) was used for the PGLS analysis after modification in Mesquite software Version 3.2 (Maddison and Maddison 2017). RMR of *L. problematicus* was then inferred from its body mass in all three scenarios. *L. problematicus* body mass was calculated following Webb (mass = $0.01L^3$, Webb 1975, following Bainbridge 1961), utilising the previously-derived estimates of body length from five specimens of *Leedsichthys* (Liston *et al*. 2013), and cross-checked with a scale model as per Motani (2001) (see Liston 2007 for full description).

Net costs of swimming (NCS) of *L. problematicus* have been 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 from Soofiani and Priede (1985), McKenzie *et al*. (2001*a*, *b*) and Lee *et al*. (2003) which relate the relative 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). Although *L. problematicus* is regarded as Neopterygii *incertae sedis* (Arratia and Schulttze 2013), a close to teleostean affinity (Arratia 2004) under true-marine conditions (Liston

2010) would be the most appropriate taxonomic and environmental parameters to employ. NCS were inferred in each case at three different swimming speeds: 0.05 body lengths * s^{-1} (as a conservative speed based on records of similar-sized living suspension-feeder fishes; see S4 Table in Ferrón 2017), 0.14 body lengths * s^{-1} (as the optimal suspension-feeding speed for a 16.5 m fish according to Weihs and Webb 1983's model) and 0.30 body lengths * s^{-1} (as the optimal cruising speed for a 16.5 m fish according to Peters 1983's approach).

RESULTS AND DISCUSSION

Maximum body sizes of living osteichthyans and chondrichthyans differ considerably. The heaviest extant bony fish (*Mola mola* with up to 2.3 tonnes; Pope *et al.* 2010) is one order of magnitude smaller than the largest cartilaginous fish (*Rhincodon typus* with up to 34 tonnes; Froese and 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 constraints of different nature have been proposed for explaining this phenomenon (see a detailed review in Freedman and 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 tons, 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 of activity, feeding strategy and body size in living organisms (Makarieva *et al.* 2005*a*, *b*, 2006; Ferrón *et al.* 2017). The high metabolic demand of bony fishes has sometimes been proposed as a possible explanation of the notorious differences in the maximum body size of living chondricthyans and osteichthyans (Freedman and Noakes 2002 and references therein). Recently, Ferrón (2017) established a methodology for assessing the locomotion energetics and metabolic constraints on body size of sharks by comparing estimates of their energetic budget (≈ routine metabolic rate, RMR) and locomotion energetic requirements (≈ net costs of swimming, NCS). Here, based on that work, we have developed a parallel methodology from living actinopterygian 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 detect a high correlation between RMR and body mass (p-value = 2.2^-16) and all points adjust properly to a linear model showing a good fit and low dispersion (R^2= 0.85) (Appendix S2). These aspects support the relationship between both variables as being well-founded, and that the analysis can be reliably used for predicting the RMR (and the energetic budget) of extinct actinopterygians. On the other hand, power performance curves calculated in small living fishes (relating the oxygen consumption and swimming speed) have been revealed as suitable models for predicting the costs of locomotion of free-swimming larger species (Sundström and 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 and 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 the established approach, the energetic budget of *L. problematicus* (i.e., RMR) considerably exceeded its locomotion costs (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. 1). Given that 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 main 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 in osteichthyans (see Freedman and 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 and 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 and 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 and 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 or chondrosteans Nelson *et al.* 2016) or have secondarily acquired this condition from bony ancestors (e.g., 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 different lineages of giant vertebrates follows similar trajectories (i.e., cetaceans, pachycormids and placoderms), where the acquisition of the largest body sizes occurs always after the apparent adaptation to suspension feeding (Friedman 2012). Therefore, ecological scenarios that prevent the occupation of such ecospaces may also hinder the evolution of gigantic body sizes. In this sense, well-established lineages of Cenozoic suspension feeder 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 osteichthyans. Despite the exceptionality 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. 2). Modifications in the mandibular aspect ratio, the loss of the 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 the patterns followed by most other groups of gigantic 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. 2). On the other hand, high local productivity of some areas (Liston 2007 and references therein) and the absence of other big suspension feeder 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 (Freedman and 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 considered as a likely scenario given the large sizes reached by its largest representatives, especially if we take into account that this reproductive strategy has repeatedly evolved throughout the evolutionary history of osteichthyans (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 osteichthyans, and the acquisition of gigantic sizes, triggering in conjunction the rise of this successful lineage of gigantic suspension feeders.

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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*. Verlag Dr. Friedrich Pfeil, München, Germany, 649 pp.

BAINBRIDGE, R. 1961. Problems of fish locomotion. 13–32. *In* Harris, J. E. (ed.). *Vertebrate Locomotion*. Zoological Society of London, London, **5**, 132 pp.

BETANCUR, R., BROUGHTON, R. E., WILEY, E. O., CARPENTER, K., LÓPEZ, J. A., LI, C., HOLCROFT, N. I., ARCILA, D., SANCIANGCO, M. and CURETON II, J. C., 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: Tree of Life*, **5**. Edition 1. doi: 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, Hoboken, New Jersey, 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*). MSc thesis. The College of William and Mary, Virginia, 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*, 1–5.

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 and 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: Biological Sciences*, **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. World Wide Web electronic publication. *www.fishbase.org*, 02/2017.

GILBERT, S. F. 2000. Osteogenesis: the development of bones. 507–510. *In* GILBERT, S.F (ed.). *Developmental biology*, 6^{th} edition, 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*. Verlag Dr. Friedrich Pfeil, München, Germany, 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). 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*. Verlag Dr. Friedrich Pfeil, München, Germany, 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*. Verlag Dr. Friedrich Pfeil, München, Germany, 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**. The Geological Society, London, 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.

— 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*. Verlag Dr. Friedrich Pfeil, München, Germany, 560 pp.

— and NOÈ, 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.

MADDISON, W. P. and MADDISON, D. R. 2017. Mesquite: a modular system for evolutionary analysis. Version 3.2 http://mesquiteproject.org

MAKARIEVA, A. M., GORSHKOV, V. G. and LI, B.-L. 2005*a*. Temperature-associated upper limits to body size in terrestrial poikilotherms. *Oikos*, **111**, 425–436.

— — —. 2005*b*. Gigantism, temperature and metabolic rate in terrestrial poikilotherms. *Proceedings of the Royal Society B: Biological Sciences*, **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. 2001*a*. 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 and Aquatic Sciences*, **58**, 1104–1112.

— — — TAYLOR, E. W., CATAUDELLA, S. and BRONZI, P. 2001*b*. Effects of acclimation to brackish water on tolerance of salinity challenge by young-of-the-year Adriatic sturgeon (*Acipenser naccarii*). *Canadian Journal of Fisheries and 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 and Outreach*, **2**, 224.

NELSON, J. S., GRANDE, T. C. and WILSON, M. V. 2016. *Fishes of the World, 5th Edition*. John Wiley & Sons, Hoboken, New Jersey, 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. The caper package: comparative analysis of phylogenetics and evolution in R. *R package version*, **5**, 1–36.

PARADIS, E., BLOMBERG, S., BOLKER, B., CLAUDE, J., CUONG, H. S., DESPER, R., DIDIER, G., DURAND, B., DUTHEIL, J. and GASCUEL, O. 2017. Package 'ape'. *Analyses of phylogenetics and evolution, version*, 2.4-1.

PETERS, R. H. 1983. *The ecological implications of body size*. Cambridge University Press, New York, 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 and 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 DEVELOPMENT CORE TEAM. 2017. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna.

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*. Verlag Dr. Friedrich Pfeil, München, Germany, 560 pp.

SCHUMACHER, B. A., SHIMADA, K., LISTON, J. J. and MALTESE, A. G. 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. doi: 10.1038/srep01471

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.

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. *Fish biomechanics*, 339–371.

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.

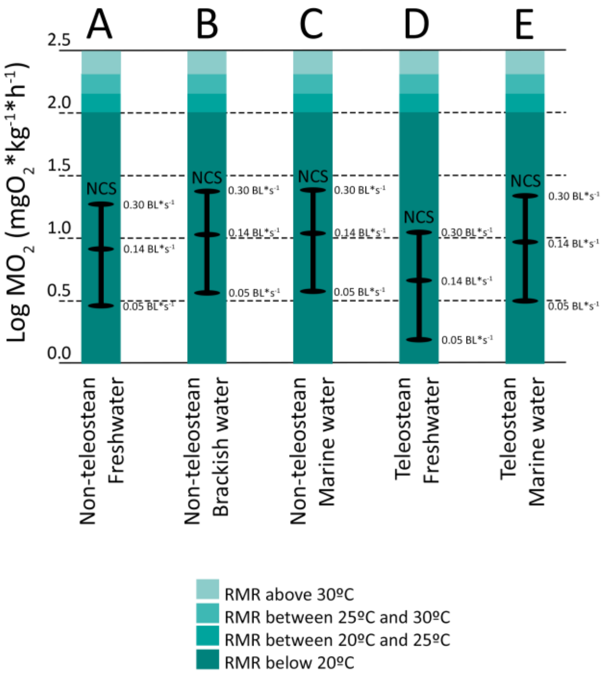


Figure 1. Comparison between routine metabolic rate (RMR) and net cost of swimming (NCS) (at 0.05, 0.14 and 0.30 body lengths*s^{-1}) of a 44.9 tons *Leedsichthys problematicus* considering different environmental and phylogenetic scenarios. Green gradation represents RMR at different water temperatures (see color code chart). NCS calculated from power-performance curves of (A, B and C) *Acipenser naccarii* from McKenzie *et al.* (2001*a*, *b*), (D) *Oncorhynchus kisutch* from Lee *et al.* (2003) and (E) *Gadus morhua* from Soofiani and Priede (1985). NCS are constant in all temperature scenarios (see text).

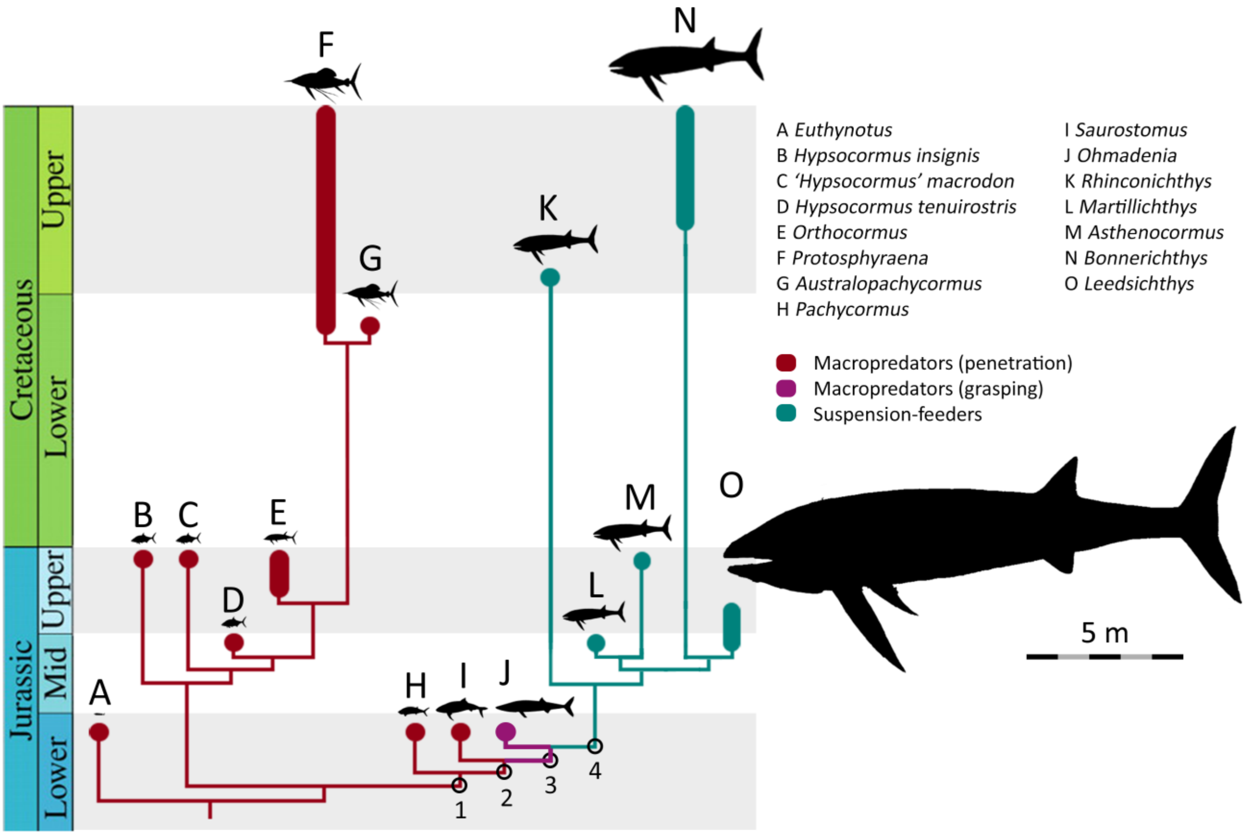


Figure 2. Main anatomical innovations and body size dynamics along the evolutionary ecological shift from macropredation to suspension feeding strategy in pachycormiforms. 1, Unossified sections in the vertebral column; 2, Unossified vertebral column and loss of some dermal skull elements; 3, Loss of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

Appendix S1. Routine metabolic rate (RMR) and body mass of actinopterygians compiled from FishBase (Froese and Pauly 2017).

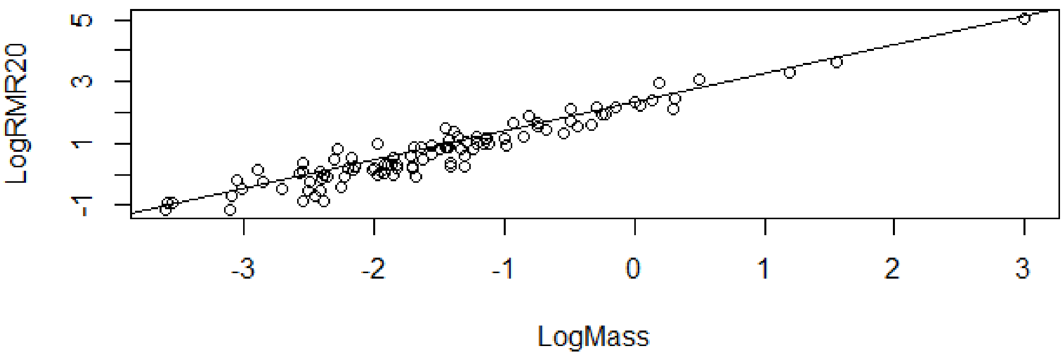
Species	Specimen in the phylogeny (Betancur et al., 2013)	Body mass (g)	Temperature (ºC)	RMR (mg O_2 kg^{-1} h^{-1})	RMR (mg O_2 h^{-1}) (20ºC)	RMR (mg O_2 h^{-1}) (25ºC)	RMR (mg O_2 h^{-1}) (30ºC)
Acipenser stellatus	G1187	1554.75	21.1	641.91	926.78	1310.67	1853.57
Ambassis interrupta	E1100	3.10	25.0	130.00	0.28	0.40	0.57
Ameiurus natalis	G1199	9.83	19.7	135.00	1.36	1.92	2.72
Anguilla rostrata	G1202	3.94	20.0	315.56	1.24	1.76	2.48
Anoplogaster cornuta	E0662	38.62	5.0	17.50	1.91	2.70	3.82
Aristostomias lunifer	E0065	21.10	5.0	14.00	0.84	1.18	1.67
Benthalbella elongata	E0033	35.30	0.3	53.00	7.33	10.37	14.66
Borostomias panamensis	E0813	103.85	7.5	35.50	8.77	12.40	17.54
Callionymus lyra	E0946	62.76	14.1	168.20	15.89	22.47	31.78
Campostoma anomalum	G1236	19.25	17.9	187.00	4.16	5.89	8.33
Caranx hippos	E0834	38.30	14.7	225.00	12.44	17.60	24.89
Centropristis striata	E0163	41.00	20.0	615.00	25.22	35.66	50.43
Channa striata	E1133	51.20	29.4	426.20	11.37	16.09	22.75
Chanos chanos	E0345	5.03	27.0	1011.88	3.13	4.43	6.26
Chelon macrolepis	E0845	6.00	29.0	262.00	0.84	1.19	1.68
Chiasmodon niger	E1115	76.60	2.5	39.00	10.05	14.21	20.10
Chromis chromis	E0201	6.31	21.5	291.75	1.66	2.35	3.33
Citharichthys stigmaeus	E0043	15.00	15.0	80.00	1.70	2.40	3.39
Conger conger	G1261	208.26	16.9	111.60	28.81	40.75	57.63
Coregonus autumnalis	G1263	154.00	7.0	202.67	77.03	108.93	154.05
Coryphaena hippurus	E0937	0.90	13.5	450.00	0.64	0.90	1.27
Cottus gobio	E0281	2.90	18.0	355.00	1.18	1.67	2.37
Cubiceps whiteleggii	E0672	1.30	13.5	650.00	1.33	1.88	2.65
Cyclothone microdon	G1272	0.78	0.3	23.00	0.07	0.10	0.14
Cyprinodon variegatus	E1066	1.42	24.3	524.71	0.56	0.79	1.11
Diplodus sargus sargus	E0807	22.88	14.0	227.50	7.89	11.16	15.78
Dorosoma cepedianum	E1016	35.30	16.3	674.19	30.76	43.50	61.51
Embiotoca lateralis	E0120	599.00	15.0	107.00	90.64	128.19	181.28
Esox masquinongy	G1289	14.02	15.0	173.44	3.44	4.86	6.88
Etheostoma rufilineatum	E0152	3.85	15.0	57.50	0.31	0.44	0.63
Fundulus heteroclitus	G1293	5.22	18.2	1068.44	6.31	8.93	12.63
Fundulus parvipinnis	E0389	4.05	19.2	183.10	0.78	1.11	1.57
Gadus morhua	E0375	2079.41	9.5	63.50	273.40	386.64	546.80
Gadus ogac	E0470	180.00	0.0	63.00	45.36	64.15	90.72
Gambusia affinis	G1296	0.29	20.2	399.11	0.11	0.16	0.23
Gasterosteus aculeatus	E1012	0.99	10.4	180.00	0.35	0.49	0.69
Girella nigricans	E0197	116.58	18.9	371.20	46.57	65.87	93.15
Gobionotothen gibberifrons	G1529	470.00	0.3	23.00	42.35	59.89	84.70
Gymnocephalus cernua	E0140	37.60	17.5	168.50	7.53	10.66	15.07
Gymnodraco acuticeps	E0155	74.40	-0.9	47.00	14.89	21.05	29.78
Gymnoscopelus opisthopterus	G1309	23.55	0.3	32.00	2.95	4.18	5.90
Heteropneustes fossilis	G1323	32.73	26.6	312.64	6.48	9.16	12.96

Kuhlia sandvicensis	E0957	58.00	23.0	147.88	6.97	9.85	13.93
Lagodon rhomboides	G1346	12.89	23.4	194.93	1.99	2.82	3.98
Leiostomus xanthurus	G1349	14.24	25.0	89.83	0.90	1.28	1.81
Lepomis cyanellus	E0132	10.00	25.0	219.67	1.55	2.20	3.11
Lepomis macrochirus	E1113	61.03	20.1	167.49	10.18	14.40	20.36
Limanda limanda	E0690	7.00	10.0	97.00	1.36	1.92	2.72
Liza richardsonii	E0808	28.21	22.1	361.77	8.83	12.49	17.66
Lota lota	E0489	213.00	11.3	74.00	28.81	40.74	57.62
Lutjanus campechanus	E0592	365.50	17.5	81.00	35.21	49.79	70.41
Macrognathus aculeatus	G1367	38.54	26.3	95.32	2.37	3.35	4.73
Melamphaes acanthomus	E0427	20.05	7.5	35.50	1.69	2.39	3.39
Melanocetus johnsonii	E0657	50.55	2.5	23.00	3.91	5.53	7.82
Micropterus salmoides	E1110	20.53	22.7	438.56	7.47	10.57	14.94
Mugil curema	E0031	44.42	22.2	427.10	16.35	23.12	32.69
Mugil cephalus	E0049	47.23	23.1	185.74	7.08	10.02	14.17
Myoxocephalus octodecemspinosus	E0221	140.98	10.0	58.75	16.56	23.43	33.13
Mystus gulio	G1387	12.00	27.0	156.00	1.15	1.63	2.30
Nannobrachium regale	E0790	2.90	5.0	16.00	0.13	0.19	0.26
Notothenia coriiceps	G1526	730.00	0.6	50.67	141.59	200.24	283.18
Oncorhynchus nerka	E0437	11.98	14.2	117.00	2.10	2.97	4.20
Oneirodes acanthias	E065	4.20	5.0	11.00	0.13	0.18	0.26
Opsanus tau	E0040	325.00	20.0	400.00	130.00	183.85	260.00
Oreochromis niloticus	G1407	100.91	25.1	215.08	15.26	21.58	30.52
Oryzias latipes	G1408	0.26	25.0	656.97	0.12	0.17	0.24
Parophrys vetulus	E0445	70.00	15.0	100.00	9.90	14.00	19.80
Perca fluviatilis	G1428	36.50	17.9	185.53	7.81	11.05	15.63
Pimephales promelas	G1439	2.00	18.0	156.50	0.36	0.51	0.72
Platichthys stellatus	E0026	15.00	15.0	100.00	2.12	3.00	4.24
Plecoglossus altivelis altivelis	G1440	10.70	19.0	801.00	9.19	12.99	18.37
Pleuronectes platessa	E0053	2.90	14.0	531.00	2.33	3.30	4.67
Poecilia latipinna	E1065	3.25	24.3	251.36	0.61	0.86	1.21
Pollachius pollachius	E0372	512.50	18.5	261.50	148.70	210.30	297.41
Pomadasys commersonnii	E0761	571.30	20.0	155.13	88.63	125.34	177.25
Pomoxis annularis	E0131	11.50	17.4	91.00	1.25	1.77	2.51
Poromitra crassiceps	E1061	10.80	2.7	28.00	1.01	1.42	2.01
Pseudopleuronectes americanus	E0035	20.11	15.6	64.67	1.77	2.50	3.54
Sagamichthys abei	E0366	5.70	5.0	23.00	0.37	0.52	0.74
Salmo salar	G1522	6.84	17.1	392.36	3.28	4.64	6.56
Sander vitreus	E1109	290.67	20.5	75.92	21.31	30.14	42.63
Scopelengys tristis	G1479	49.80	5.0	13.00	1.83	2.59	3.66
Scopelogadus mizolepis	E0670	3.60	5.0	20.00	0.20	0.29	0.41
Scophthalmus maximus	E1161	320.00	15.0	114.00	51.59	72.96	103.18
Scorpaena porcus	E0512	28.15	18.1	137.50	4.43	6.27	8.86
Serranus scriba	E0322	4.10	16.0	166.00	0.90	1.27	1.80
Solea solea	E0054	73.00	17.6	174.50	15.06	21.30	30.12
Spinachia spinachia	G1491	2.65	18.3	354.00	1.06	1.50	2.12
Stenobrachius	E0067	4.35	7.5	80.00	0.83	1.17	1.66

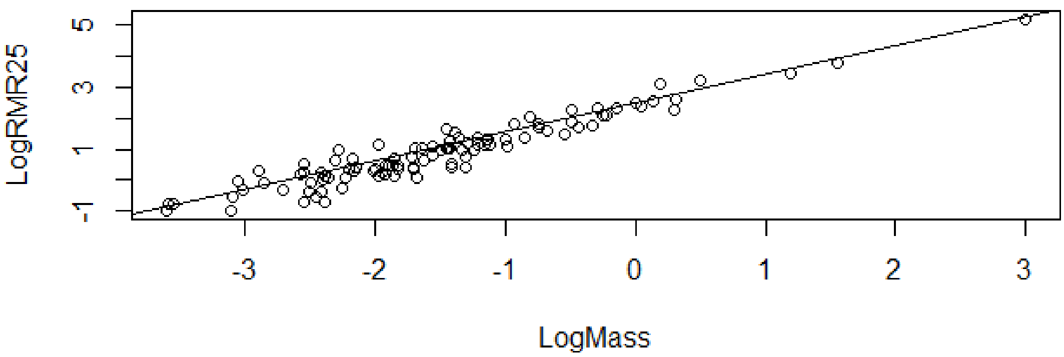
leucopsarus							
Stomias danae	E0037	13.80	2.5	42.00	1.95	2.76	3.90
Symbolophorus californiensis	E0061	0.80	5.0	86.00	0.19	0.28	0.39
Syngnathus acus	E0821	7.30	18.5	236.50	1.92	2.71	3.83
Trematomus pennellii	G1527	183.00	-0.9	43.00	33.50	47.38	67.00
Zoarces viviparus	E0370	0.25	5.0	103.50	0.07	0.10	0.15

Appendix S2. Phylogenetic generalized least squares analyses between routine metabolic rate (RMR) and body mass of actinopterygians at three different temperature scenarios.

20ºC LogRMR (20ºC) = 2.344724 + 0.926953*LogMass $R^2 = 0.85$



25ºC LogRMR (25ºC) = 2.495239 + 0.926953*LogMass $R^2 = 0.85$



30ºC LogRMR (30ºC) = 2.645754 + 0.926953*LogMass $R^2 = 0.85$