Report

Current Biology

Bite Force in the Extant Coelacanth *Latimeria*: The Role of the Intracranial Joint and the Basicranial Muscle

Highlights

- The coelacanth *Latimeria* possesses an intracranial joint and a basicranial muscle
- We show that these unique features enhance bite force
- A high bite force likely allows *Latimeria* to feed on a wide range of prey

Authors

Hugo Dutel, Marc Herbin, Gaël Clément, Anthony Herrel

Correspondence

hugo.dutel@riken.jp

In Brief

Dutel et al. present a biomechanical model of the skull of *Latimeria* that suggests that the intracranial joint and the basicranial muscle enhance the overall bite force. These results shed light on the role in prey capture of these anatomical features, which are found only in *Latimeria* among living vertebrates.

Dutel et al., 2015, Current Biology *25*, 1228–1233
May 4, 2015
http://dx.doi.org/10.1016/j.cub.2015.02.076

CellPress

Bite Force in the Extant Coelacanth *Latimeria*: The Role of the Intracranial Joint and the Basicranial Muscle

Hugo Dutel,[1],* Marc Herbin,[2] Gaël Clément,[3] and Anthony Herrel[2,4]
[1]RIKEN Evolutionary Morphology Laboratory, Kobe Hyogo 650-0047, Japan
[2]UMR 7179 CNRS-MNHN, Mécanismes Adaptatifs: des Organismes aux Communautés, Département Écologie et Gestion de la Biodiversité, Muséum National d'Histoire Naturelle, 75231 Paris, France
[3]Centre de Recherche sur la Paléobiodiversité et les Paléoenvironnements (CR2P, UMR 7207), Sorbonne Universités, MNHN, CNRS, UPMC-Paris 6, Muséum National d'Histoire Naturelle, 57 rue Cuvier, CP38, 75005 Paris, France
[4]Evolutionary Morphology of Vertebrates, Ghent University, K.L. Ledeganckstraat 35, 9000 Gent, Belgium
*Correspondence: hugo.dutel@riken.jp
http://dx.doi.org/10.1016/j.cub.2015.02.076

SUMMARY

The terrestrialization process involved dramatic changes in the cranial anatomy of vertebrates. The braincase, which was initially divided into two portions by the intracranial joint in sarcopterygian fishes, became consolidated into a single unit in tetrapods and lungfishes [1–3]. The coelacanth *Latimeria* is the only extant vertebrate that retains an intracranial joint, which is associated with a unique paired muscle: the basicranial muscle. The intracranial joint has long been thought to be involved in suction feeding by allowing an extensive elevation of the anterior portion of the skull, followed by its rapid depression driven by the basicranial muscle [4–7]. However, we recently challenged this hypothesis [8, 9], and the role of the basicranial muscle with respect to the intracranial joint thus remains unclear. Using 3D biomechanical modeling, we show here that the basicranial muscle and the intracranial joint are involved in biting force generation. By flexing the anterior portion of the skull at the level of the intracranial joint, the basicranial muscle increases the overall bite force. This likely allows *Latimeria* to feed on a broad range of preys [10, 11] and coelacanths to colonize a wide range of environments during their evolution [4]. The variation in the morphology of the intracranial joint observed in Devonian lobe-finned fishes would have impacted to various degrees their biting performance and might have permitted feeding specializations despite the stability in their lower jaw morphology [12].

RESULTS AND DISCUSSION

The living coelacanth *Latimeria*, a rare marine lobe-finned fish reaching up to 2 m in length, is the only extant representative of the Actinistia, a group of sarcopterygian fishes that originated in the Devonian and was thought to be extinct for 75 million years (Figure 1A). Although the living *Latimeria* has been extensively studied since its discovery in 1938, many aspects of its biology and ecology remain virtually unknown due to its deep-sea habitat [4]. In an evolutionary context, *Latimeria* has long been of key interest for our understanding of the "fish-to-tetrapod" transition since it is considered as the sister group of all other extant sarcopterygians (tetrapods + lungfishes, Figure 1B) [4, 14]. Notably, it possesses some ancestral anatomical features of sarcopterygians that have been independently lost in tetrapods and lungfishes [1–3] (Figure 1B). One of these features, the intracranial joint (Figures 1C–1E), likely has a major impact on the biomechanics of the skull during prey capture.

In *Latimeria*, the intracranial joint divides the neurocranium into two portions, an anterior (ethmosphenoid portion) and posterior (otoccipital portion) one, and is associated with a paired basicranial muscle spanning the joint ventrally along the length of the neurocranium (Figures 1D and 1E). This joint was thought to allow an elevation of the snout by 15° to 20° relative to the posterior portion of the skull, thereby enlarging the gape and allowing for powerful suction [4–7]. In previous functional models, the basicranial muscle was thought to depress the anterior portion of the skull from its elevated state, returning it to its resting position [4–7]. However, a recent re-description of the anatomy of *Latimeria* has demonstrated that there is no clear mechanism that could drive the elevation of the anterior portion of the skull [8, 9]. By contrast, a distinct ventroflexion of the anterior portion of the skull from its resting position under the action of the basicranial muscle is anatomically permitted [8] and was reported in a living specimen [15]. As such, we suggest that the intracranial joint and the basicranial muscle are associated with an enhancement of bite force rather than mouth closure during suction feeding.

To estimate the theoretical bite force and muscle contribution in bite force generation, we computed a 3D static force equilibrium model [16] based on an X-ray computed microtomography acquisition (μCT scan) of an adult specimen (Figure 2) and detailed anatomical descriptions of the cranial muscles [8, 9]. Muscle forces were calculated based on their physiological cross-section area (PCSA) obtained after dissection of the same specimen and their 3D coordinates of origin and insertion (see [8], Supplemental Experimental Procedures, and Table S1).

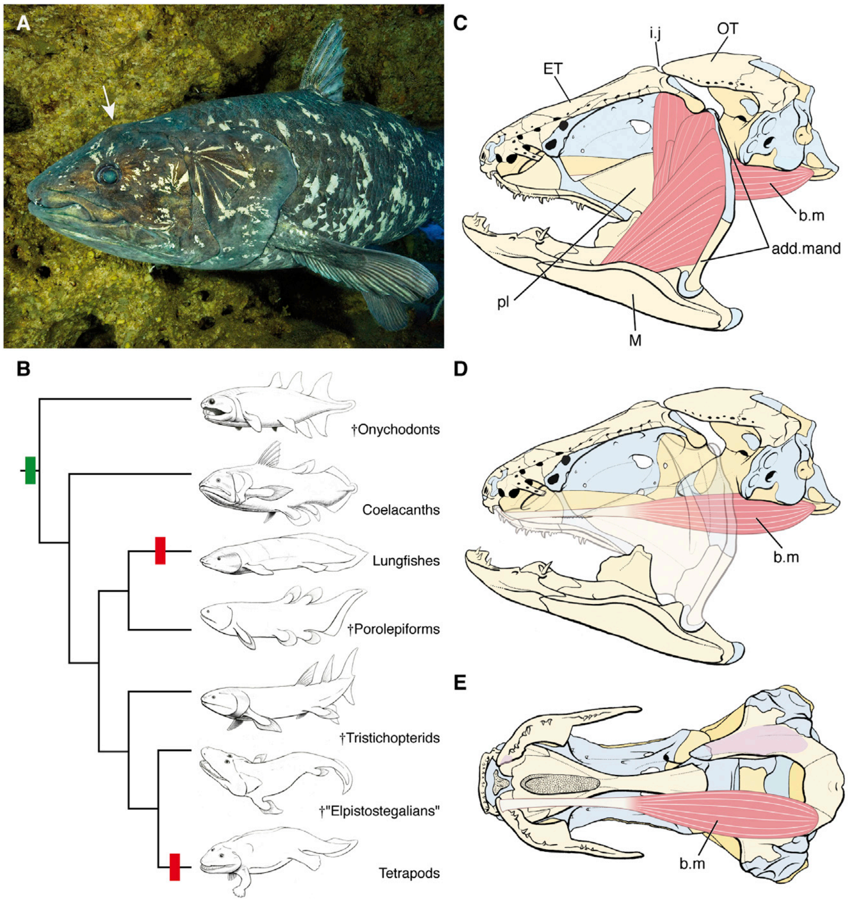

Figure 1. *Latimeria chalumnae* Smith 1939

(A) The living coelacanth *Latimeria* in its natural environment at 113 m of depth at Sodwana Bay, iSimangaliso Wetland Park, South Africa. The arrow indicates the position of the intracranial joint (photograph courtesy of Laurent Ballesta, Andromède Océanologie).

(B) Simplified phylogeny of sarcopterygian vertebrates based on [13] showing the interrelationships between onychodonts (*Onychodus*), coelacanths (*Latimeria*), lungfishes (*Neoceratodus*), porolepiforms (*Holoptychius*), tristichopterids (*Eusthenopteron*), "elpistostegalians" (*Tiktaalik*), and tetrapods (*Ichthyostega*). Fossil taxa are indicated by a dagger. The intracranial joint is a synapomorphy (i.e., a unique derived feature) of sarcopterygians (green vertical dash), which has been independently lost in lungfishes and tetrapods (red vertical dash). The coelacanth *Latimeria* is the only extant vertebrate with an intracranial joint.

(C and D) Left lateral views of the skull showing the jaw-closing muscles and the basicranial muscle.

(E) Ventral view of the skull showing the basicranial muscle. The purple coloration indicates the areas of origin and insertion of the basicranial muscle on the ventral surface of the neurocranium.

Abbreviations used are as follows: add. mand., adductor mandibulae; b.m., basicranial muscle; ET, ethmosphenoid portion of the skull; i.j., intracranial joint; M, mandible; OT, otoccipital portion of the skull; pl, palate. See also Table S1.

Bite force was calculated for an anterior and a posterior biting point on the mandible and the anterior portion of the skull (Figure 2A). Our model involves two mobile joints, the palate-mandibular joint and the intracranial joint (Figure 2A). The joint between the palate and the ethmosphenoid portion of the skull is considered as fixed since it permits only slight movements in the transverse plane [8]. As such, the unit moving around the intracranial joint consists of the ethmosphenoid portion of the skull, the palate and the mandible. The intracranial joint thus essentially causes the "face" to rotate relative to the back of the skull. To assess the role of the basicranial muscle and intracranial joint in biting force generation, we considered the following scenarios. First, we calculated the biting force generated by the adductor mandibulae muscle (m. adductor mandibulae) only when the mandible was depressed over gapes ranging from 5° to 30° (Figure 2A, add. mand.). Then, we considered that the action of the m. adductor mandibulae was accompanied by a flexion of 5° (Figure 2A, intracranial joint [I.J.] = 5) and 10° (Figure 2A, I.J = 10) of the front of the skull around the intracranial joint under the action of the basicranial muscle.

The bite force generated by the m. adductor mandibulae increased with gape angle (Figure 2B), and the jaw system of *Latimeria* thus appeared to be optimized for biting at a relatively high gape angle. At a gape of 25°, the bite force generated by the m. adductor mandibulae reached a plateau and was estimated to be 228 newtons (N) at the front of the mandible (bite point 1) and 295 N at the level of the hook-shaped process of the dentary (bite point 2). Since more posterior biting points result in a shorter outlever of the mandible, this resulted in an increase in bite force (Figure 2C). The contribution of the basicranial muscle to the overall bite force increased with an increasing ventroflexion of the anterior portion of the skull. The action of the basicranial muscle produced a force ranging from 138 N (bite point 1) to 151 N (bite point 2) for a 5° ventroflexion and 169 N (bite point 1) to 186 N (bite point 2) for a 10° ventroflexion (Figure 2C). At a 25° gape, the flexion of the anterior portion of the skull at the level of the intracranial joint from its resting position under the action of the basicranial muscle increased the theoretical bite force at the level of bite point 1 by 60% (for a 5° flexion) to 74% (for a 10° flexion) relative to the condition when only the m. adductor mandibulae was considered (Figure 2D). The inclusion of the basicranial muscle in the model resulted in a total biting force ranging from 366 N (bite point 1) to 447 N (bite point 2) when the intracranial joint was flexed by 5° and 397 N (bite point 1) to 481 N (bite point 2) for a 10° flexion (Figure 2C). Since the bite force generated by the m. adductor mandibulae decreased as the jaw closed, the relative contribution of the basicranial muscle to the overall bite force was higher at lower gapes (Figure 2D).

A comparison with a large range of vertebrate taxa (Figure 3A, Supplemental Experimental Procedures, and Table S2) shows that the bite force of *Latimeria* is intermediate for its body length when only the action of the jaw adductors is considered. By contrast, *Latimeria* has a high bite force for its length when the basicranial muscle is included in the calculations.

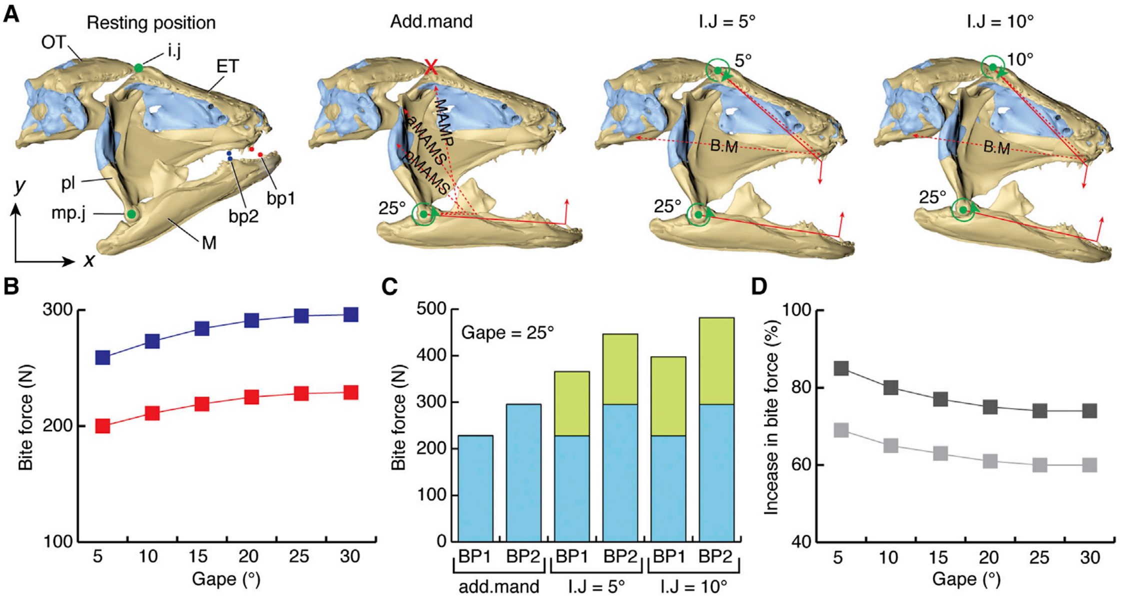

Figure 2. Biting Model of *Latimeria chalumnae* Smith 1939

(A) Skull in right lateral view showing the position of the anterior (bp1) and posterior (bp2) bite points on the mandible and the anterior portion of the skull. Bite force was first calculated for a given gape (here 25°) using the forces and the directions of the bundles of m. adductor mandibulae only. Next, the bite force was calculated for a combined action of the m. adductor mandibulae and basicranial muscles when the anterior portion of the skull (ET + pl + M) was flexed by 5° (I.J. = 5) and 10° (I.J. = 10). Dashed line represents the line of action of the muscles and the input moment arm. Solid line represents the output moment arm and the bite force generated by the muscles.

(B) Bite force (N) generated by the m. adductor mandibulae versus gape angle (°) at bite point 1 (red) and bite point 2 (blue).

(C) Output of the bite model for a 25° gape at bite point 1 and 2 when only the action of the m. adductor mandibulae is considered (add. mand.) and when the intracranial joint is flexed by 5° (I.J. = 5) and 10° (I.J. = 10).

(D) Proportional increase in bite force at bite point 1 arising from the action of the basicranial muscle when the intracranial joint is flexed by 5° (gray) and 10° (black) plotted against gape angle (°).

Abbreviations used are as follows: add. mand., m. adductor mandibulae; aMAMS, anterolateral bundle of the m. adductor mandibulae superficialis; B.M., basicranial muscle; bp1 and bp2, bite points 1 and 2; ET, ethmosphenoid portion of the skull; i.j., intracranial joint; M, mandible; MAMP, m. adductor mandibulae profundus; mp.j., mandible-palatal joint; OT, otoccipital portion of the skull; pl, palate; pMAMS, posterolateral bundle of the m. adductor mandibulae superficialis. See also Supplemental Experimental Procedures and Table S1.

Surprisingly, *Latimeria* stands in contrast to actinopterygians and amphibians, which have a low bite force relative to their standard length (Figure 3A), but falls alongside top predators such as bull sharks [18]. Comparatively, a bull shark of the same length as the specimen of *Latimeria* used in this study would generate a biting force of 613 N. However, if this species possessed the force-enhancing effect of an intracranial joint and basicranial muscle as *Latimeria* does, its bite force would be pushed up to 1,068 N.

Latimeria possessed one of the highest bite forces relative to its head width, even when the contribution of the basicranial muscle was not included in our calculation of bite force (Figure 3B). Head width scaled positively with bite force (Figure 3B) and was the only predictor of bite force after removing the effect of body mass (Supplemental Experimental Procedures). This is likely due to the fact that wider heads allow for the presence of larger jaw adductors [18]. Nonetheless, enlarged jaw adductors may negatively impact other performance traits such as suction feeding and locomotion, thus resulting in evolutionary trade-offs [19]. Indeed, head width scales at a higher degree with body length in fishes (non-tetrapod vertebrates) than in tetrapods, probably because of the need for a streamlined head to move in a denser environment (Figure 3C). However, when compared to other fishes (non-tetrapod vertebrates), *Latimeria* still retained a relatively high bite force relative to its head width but stood out as possessing a narrow head width relative to its body length (Figure 3C). Therefore, the presence of a basicranial muscle running ventral to the neurocranium can be seen as a way to accommodate more muscle beyond the limitations imposed by the need for a streamlined head and large gape.

Stomach contents of *Latimeria* indicate that it feeds on a wide variety of prey [10, 11], including deep-sea fishes and cephalopods. Prey items retrieved from stomach contents show a wide range of sizes and hardness (e.g., cephalopods versus sharks), suggesting that *Latimeria* is an opportunistic predator [11]. Moreover, these prey items show little traces of prey reduction, indicating that the small, pointed, and posteriorly curved teeth of *Latimeria* are used for gripping rather than slicing. In vertebrates, high bite forces relative to body size are associated with dietary specializations, such as the consumption of proportionally large and hard prey items. Indeed, larger and harder prey items require higher bite forces to capture and maintain, which likely has important consequences for diet selection [20, 21]. As such, we suggest that the high relative bite force made possible by the presence of an intracranial joint and a basicranial

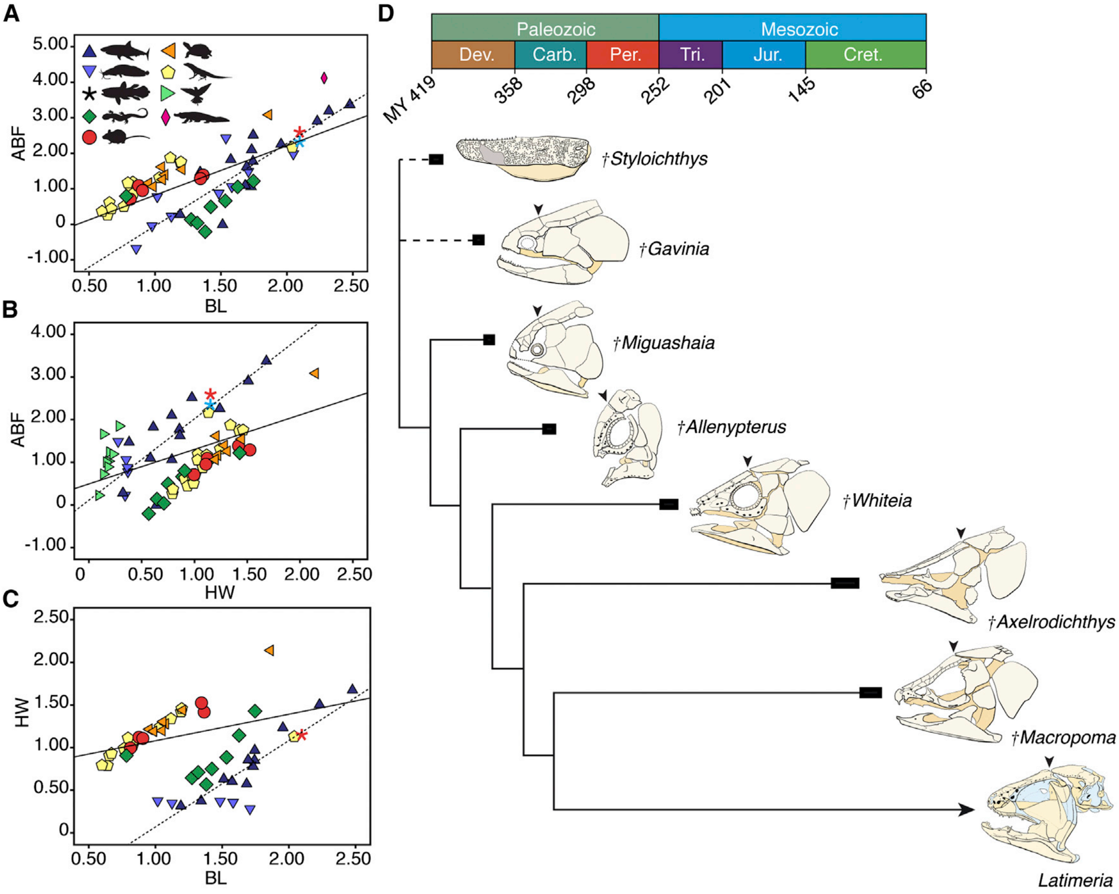

Figure 3. Relationship between Morphometric Data and Bite Force Measurements in Vertebrates

(A) Bite force versus standard length in vertebrates (solid line, $R^2 = 0.508$; slope = 1.391; $p < 0.0001$) and fishes only (dashed line, $R^2 = 0.778$; slope = 2.269; $p < 0.0001$).

(B) Bite force versus head width in vertebrates (solid line, $R^2 = 0.242$; slope = 0.809; $p < 0.0001$) and fishes only (dashed line, $R^2 = 0.699$; slope = 1.876; $p < 0.0001$).

(C) Head width versus standard length in tetrapods (solid line, $R^2 = 0.147$; slope = 0.319; $p = 0.021$) and in fishes (dashed line, $R^2 = 0.789$; slope = 1.019; $p < 0.0001$).

(D) Time-scaled phylogeny based on [17] showing the evolution of the skull and jaw across coelacanth evolution. Skulls are represented in left lateral view. Arrow indicates the position of the intracranial joint.

Note for (A)–(C) that all measurement are $\log_{10}$ transformed. Dark blue triangle indicates Chondrichthyes; light blue triangle indicates Actinopterygii; red star indicates *Latimeria* with basicranial muscle included in the calculation of the biting force; blue star indicates *Latimeria* with basicranial muscle excluded in the calculation of the biting force; green diamond indicates Amphibia; orange circle indicates Mammalia; orange triangle indicates Testudines; yellow hexagon indicates Lepidosauria; green triangle indicates Aves; purple diamond indicates Crocodylia.

See also Supplemental Experimental Procedures and Table S2.

muscle provides *Latimeria* with a wide dietary breadth and allows it to consume prey differing in size and hardness.

Our present results on *Latimeria* provide new insights allowing us to interpret the functional implications of the changes in the skull of coelacanth over geological time. Early coelacanths from the Paleozoic retain ancestral sarcopterygian features in having a short snout and a heavily ossified skull [4, 22–24], whereas more “derived” Mesozoic coelacanths have a proportionally longer anterior portion of the skull relative to the posterior one (Figure 3D). During coelacanth evolution, the anterior shift of the insertion of the basicranial muscle from the posterior margin of the parasphenoid to the tip of the anterior portion of the skull might have increased its mechanical advantage and may have yielded higher bite forces. The lengthening of the processus connectens (i.e., the surface of the ethmosphenoid portion, which articulates with the otoccipital portion of the skull) [4], would have increased the range of movement of the front of the skull around the intracranial joint. In addition, coelacanths evolved more elongate jaws, with a reduced tooth row and a lower adductor force transmission [4, 13] (Figure 3D). Indeed, the jaw-closing mechanical advantage (MA) in early coelacanths (with the exception of *Gavinia*) *Diplocercides* (MA = 0.29), *Miguashaia* (MA = 0.32), and the possible coelacanth *Styloichthys* (MA = 0.28) [12] is higher than that of *Latimeria* (MA = 0.24). The evolution of longer skulls and longer mandibles along with low MA might have increased gape and allowed for a more powerful and faster suction for feeding [25] and probably respiration since air-breathing capability was inferred in fossil coelacanths [26]. By contrast, these changes might have negatively impacted bite force [25]. However, the development of the basicranial muscle in conjunction with the intracranial joint could have allowed coelacanths to circumvent the trade-offs associated with these demands. The benefits arising from a cranial morphology that accommodates both suction and biting performances might have allowed Mesozoic coelacanths to feed on a larger spectrum of prey in a broad range of aquatic environments [4, 17].

The intracranial joint is an ancestral feature of sarcopterygians, but it is absent in lungfish and tetrapods (Figure 1B), where the ethmosphenoid and otoccipital regions of the skull are firmly fused [1, 3, 27]. When present, the intracranial joint in sarcopterygian fishes deviates to different degrees from the generalized ancestral morphology. In Paleozoic sarcopterygian fishes, the presence of insertion scars on the ventral surface of the otoccipital portion of the skull, such as in the coelacanth *Diplocercides* [4], the onychodonts *Onychodus* and *Qingmenodus* [28, 29], the tristichopterid *Eusthenopteron* [27, 30], and the osteolepidid *Gogonasus* [31], suggested that it was associated with the presence of a basicranial muscle. The intracranial joint is considered as clearly mobile in coelacanths and onychodonts [28, 29], where the two halves of the skull are separated and articulated by a well-developed otic shelf. By contrast, it was likely less mobile in stem sarcopterygians as well as in the osteolepid *Gogonasus* and immobile in the porolepiform *Powichthys*, in which the ethmosphenoid and otoccipital dermal shields are sutured [32, 33]. Additionally, the basicranial muscle varies in length among taxa and is shorter in most sarcopterygian fishes than in coelacanths and onychonts [28, 29].

The variability in the intracranial joint anatomy across sarcopterygian fishes suggests various degrees of biting performance, which might have resulted in a different dietary scope despite the relative biomechanical stability of the lower jaw [12]. As in *Latimeria*, the presence of a kinetic intracranial joint and a basicranial muscle in sarcopterygian fishes might have played a role in prey capture. However, shorter basicranial muscle and reduced mobility of the intracranial joint in stem sarcopterygian fishes and rhipidistians might have yielded relatively smaller moment compared to *Latimeria*, and potentially onychodonts. The variability in the skull anatomy contrasts with the relative morphological stability of the lower jaw of most sarcopterygian fishes and early tetrapods, which retain gracile jaws bearing slender, pointed cusps [12]. Among tetrapodomorphs, the loss of a kinetic intracranial joint and the evolution of broad, flattened skulls in the Devonian elpistostegalians *Panderichthys* [1], *Tiktaalik* [2], and early tetrapods [27] might have affected their bite performance. Indeed, poor biting capacities were inferred in early tetrapods [34], and in vivo data of modern analogs rather suggest that their morphology is associated with jaw-powered suction feeding under water [35] or with grabbing prey on land with subsequent aquatic hydrodynamic transport [36]. Moreover, the discrepancy in the biting performance between basal tetrapods and amniotes as well as the delay in the development of a jaw morphology tuned to biting [37] suggest that novel mechanisms enhancing biting performances evolved much later as a response to selective pressures after the colonization of land.

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures and two tables and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2015.02.076.

AUTHOR CONTRIBUTIONS

All authors contributed to the project concept and design. H.D., A.H., and M.H. acquired the data. H.D. analyzed the data, wrote the manuscript, and made the scientific illustrations. A.H. provided unpublished comparative data on bite force in vertebrates. A.H., G.C., and M.H. provided critical reviews and discussion during the manuscript development. All authors approved the final draft.

ACKNOWLEDGMENTS

We thank Miguel Garcia Sanz for performing the X-ray tomography acquisitions at the CT scan facility AST-RX, plate-forme d'accès scientifique à la tomographie à rayons X du MNHN, Paris in the USM 2700 outils et méthodes de systématique integrative CNRS-MNHN; Florent Goussard (MNHN) and Damien Germain (MNHN) for their help in handling the raw 3D data. 3D modeling work was performed at the Atelier de tomosynthèse, CR2P UMR MNHN/CNRS/UPMC-Paris 6; Philippe Janvier (MNHN) for his useful comments during the writing of this manuscript; Laurent Ballesta (Andromède Océanologie) for the photograph in Figure 1A; Julien Claes (UCL, Belgium) for providing part of the measurements made on chondrichthyans; and Céline Bens and Tarik Afoukati, Collections de Pièces anatomiques en Fluides of the MNHN, for their help in the preparation of the *Latimeria* specimen for dissection and CT scanning. This work is a contribution to the ANR TERRES Programme (ANR-2010-BLAN-607-03) and LabEx ANR-10-LABX-0003-BCDiv, in the frame of the Programme Investissements d'avenir n° ANR-11-IDEX-0004-02.

Received: October 8, 2014
Revised: January 25, 2015
Accepted: February 26, 2015
Published: April 16, 2015

REFERENCES

1. Ahlberg, P.E., Clack, J.A., and Luksevics, E. (1996). Rapid braincase evolution between *Panderichthys* and the earliest tetrapods. Nature *381*, 61–64.
2. Downs, J.P., Daeschler, E.B., Jenkins, F.A., Jr., and Shubin, N.H. (2008). The cranial endoskeleton of *Tiktaalik roseae*. Nature *455*, 925–929.
3. Friedman, M., and Brazeau, M.D. (2010). A reappraisal of the origin and basal radiation of the Osteichthyes. J. Vertebr. Paleontol. *30*, 36–56.
4. Forey, P.L. (1998). History of the Coelacanth Fishes. (London: Chapman and Hall).
5. Lauder, G.V., Jr. (1980). The role of the hyoid apparatus in the feeding mechanism of the coelacanth *Latimeria chalumnae*. Copeia *1980*, 1–9.
6. Robineau, D., and Anthony, J. (1973). Biomécanique du crâne de *Latimeria chalumnae* (Poisson crossoptérygien coelacanthidé). C. R. Acad. Sci. Paris Série D *276*, 1305–1308.
7. Thomson, K.S. (1967). Mechanisms of intracranial kinetics in fossil rhipidistian fishes (Crossopterygii) and their relatives. Zool. J. Linn. Soc. *46*, 223–253.
8. Dutel, H., Herrel, A., Clément, G., and Herbin, M. (2013). A reevaluation of the anatomy of the jaw-closing system in the extant coelacanth *Latimeria chalumnae*. Naturwissenschaften *100*, 1007–1022.
9. Dutel, H., Herrel, A., Clément, G., and Herbin, M. (2015). Redescription of the hyoid apparatus and associated musculature in the extant coelacanth *Latimeria chalumnae*: functional implications for feeding. Anat. Rec. (Hoboken) *298*, 579–601.
10. Uyeno, T. (1991). Observations on locomotion and feeding of released coelacanths, *Latimeria chalumnae*. Environ. Biol. Fishes *32*, 267–273.

11. Uyeno, T., and Tsutsumi, T. (1991). Stomach contents of *Latimeria chalumnae* and further notes on its feeding habits. Environ. Biol. Fishes *32*, 275–279.
12. Anderson, P.S.L., Friedman, M., Brazeau, M.D., and Rayfield, E.J. (2011). Initial radiation of jaws demonstrated stability despite faunal and environmental change. Nature *476*, 206–209.
13. Friedman, M. (2007). *Styloichthys* as the oldest coelacanth: implications for early osteichthyan interrelationships. J. Syst. Palaeontology *5*, 289–343.
14. Amemiya, C.T., Alföldi, J., Lee, A.P., Fan, S., Philippe, H., Maccallum, I., Braasch, I., Manousaki, T., Schneider, I., Rohner, N., *et al*. (2013). The African coelacanth genome provides insights into tetrapod evolution. Nature *496*, 311–316.
15. Thomson, K.S. (1973). New observations on the coelacanth fish *Latimeria chalumnae*. Copeia *1973*, 813–814.
16. Cleurens, J., Aerts, P., and De Vree, F. (1995). Bite and joint force analysis in *Caiman crocodilus*. Belg. J. Zool. *125*, 79–94.
17. Dutel, H., Maisey, J.G., Schwimmer, D.R., Janvier, P., Herbin, M., and Clément, G. (2012). The giant cretaceous Coelacanth (Actinistia, Sarcopterygii) *Megalocoelacanthus dobiei* Schwimmer, Stewart & Williams, 1994, and its bearing on Latimerioidei interrelationships. PLoS ONE *7*, e49911.
18. Huber, D.R., Claes, J.M., Mallefet, J., and Herrel, A. (2009). Is extreme bite performance associated with extreme morphologies in sharks? Physiol. Biochem. Zool. *82*, 20–28.
19. Van Wassenbergh, S., Herrel, A., Adriaens, D., and Aerts, P. (2004). Effects of jaw adductor hypertrophy on buccal expansions during feeding of air breathing catfishes (Teleostei, Clariidae). Zoomorphology *123*, 81–93.
20. Herrel, A., Adriaens, D., Verraes, W., and Aerts, P. (2002). Bite performance in clariid fishes with hypertrophied jaw adductors as deduced by bite modeling. J. Morphol. *253*, 196–205.
21. Huysentruyt, F., Adriaens, D., Teugels, G.G., Devaere, S., Herrel, A., Verraes, W., and Aerts, P. (2002). Diet composition in relation to morphology in some African anguilliform clariid catfishes. Belg. J. Zool. *134*, 25–30.
22. Friedman, M., and Coates, M.I. (2006). A newly recognized fossil coelacanth highlights the early morphological diversification of the clade. Proc. Biol. Sci. *273*, 245–250.
23. Zhu, M., Yu, X., Lu, J., Qiao, T., Zhao, W., and Jia, L. (2012). Earliest known coelacanth skull extends the range of anatomically modern coelacanths to the Early Devonian. Nat. Commun. *3*, 772. http://dx.doi.org/10.1038/ncomms1764.
24. Long, J.A. (1999). A new genus of fossil coelacanth (Osteichthyes: Coelacanthiformes) from the Middle Devonian of southeastern Australia. Rec. West. Aust. Mus. Suppl. *57*, 37–54.
25. Westneat, M.W. (2006). Skull biomechanics and suction feeding in fishes. In Fish Biomechanics, R.E. Shadwick and G.V. Lauder, Jr., eds. (Amsterdam: Elsevier Inc.), pp. 29–76.
26. Brito, P.M., Meunier, F.J., Clément, G., and Geffard-Kuriyama, D. (2010). The histological structure of the calcified lung of the fossil coelacanth *Axelrodichthys araripensis* (Actinistia: Mawsoniidae). Palaeontology *53*, 1281–1290.
27. Janvier, P. (1996). Early Vertebrates. (Oxford: Clarendon Press).
28. Andrews, S.M., Long, J.A., Ahlberg, P.E., Barwick, R.E., and Campbell, K. (2006). The structure of the sarcopterygian *Onychodus jandemarrai* n. sp. from Gogo, Western Australia: with a functional interpretation of the skeleton. Trans. R. Soc. Edinb. Earth Sci. *96*, 197–307.
29. Lu, J., and Zhu, M. (2010). An onychodont fish (Osteichthyes, Sarcopterygii) from the Early Devonian of China, and the evolution of the Onychodontiformes. Proc. Biol. Sci. *277*, 293–299.
30. Jarvik, E. (1980). Basic Structure and Evolution of Vertebrates, *Volume 1*. (London: Academic Press).
31. Long, J.A., Barwick, R.E., and Campbell, K.S.W. (1997). Osteology and functional morphology of the osteolepiform fish *Gogonasus andrewsae* Long, 1985, from the Upper Devonian Gogo Formation, Western Australia. Rec. West. Aust. Mus. Suppl. *53*, 1–89.
32. Ahlberg, P.E. (1991). A re-examination of sarcopterygian interrelationships, with special reference to the Porolepiformes. Zool. J. Linn. Soc. *103*, 241–287.
33. Jessen, H.L. (1980). Lower Devonian Porolepiformes from the Canadian Arctic with special reference to Powichthys thorsteinssoni. Palaeontogr. Abt. A Palaeozool-Stratigr. *167*, 180–214.
34. Neenan, J.M., Ruta, M., Clack, J.A., and Rayfield, E.J. (2014). Feeding biomechanics in *Acanthostega* and across the fish-tetrapod transition. Proc. Biol. Sci. *281*, 20132689.
35. Heiss, E., Natchev, N., Gumpenberger, M., Weissenbacher, A., and Van Wassenbergh, S. (2013). Biomechanics and hydrodynamics of prey capture in the Chinese giant salamander reveal a high-performance jaw-powered suction feeding mechanism. J. R. Soc. Interface *10*, 20121028.
36. Van Wassenbergh, S. (2013). Kinematics of terrestrial capture of prey by the eel-catfish *Channallabes apus*. Integr. Comp. Biol. *53*, 258–268.
37. Anderson, P.S.L., Friedman, M., and Ruta, M. (2013). Late to the table: diversification of tetrapod mandibular biomechanics lagged behind the evolution of terrestriality. Integr. Comp. Biol. *53*, 197–208.