

The simple morphology of the sunfish heart

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Abstract

The evolutionary conservation of the building plan of the heart suggests this organ is under substantial form–function constraints. Its form varies to such a degree, however, that it questions whether we understand the form–function relations of the heart. A previously published image of the heart of the sunfish (*Mola mola*, Tetraodontiformes) indicates the presence of an exceptionally simple topology of the chambers. Here, we describe the gross morphology of the sunfish heart ($N=7$) because, we assess, this expands the known spectrum of cardiac form that is compatible with function. The usual teleost piscine compartments were present, guarded by valved junctions: sinus venosus, atrium, ventricle, and bulbus arteriosus. Especially, the ventricle was much displaced ventrally and the atrium was dorso-ventrally elongate. The ventricular central cavity exhibited a simple 90-degree curve, or a quarter circle, and opened into an almost vertical bulbus arteriosus. Overall, the normal piscine S-topology of the cardiac chambers (when seen from the left) appeared distorted to a simpler J-shape. When compared to other fish, including a tetraodontiform boxfish, these highly unusual characters appeared to have evolved recently. The distantly related spotted tinselfish (*Xenolepidichthys dalgleyi*) resembles sunfish in shape, its heart is almost J-shaped, but the ventricle was sac-like and typically piscine. Surprisingly, the ventricular wall had a comparatively high proportion of compact myocardium, approximately 34%. The relative mass of the sunfish heart was typically piscine, approximately 0.08% of body mass. In conclusion, the sunfish heart may be the least curved cardiac structure described for any fully formed vertebrate.

KEYWORDS

cardiac looping, fish, ventricle

1 | INTRODUCTION

Anatomists have long recognized similarities between vertebrate hearts and these insights were expanded on by Keith and Flack to formalize a fairly detailed, and still valid, conserved building plan of the heart (Keith & Flack, 1907). The heart first and foremost imparts energy to the blood in the form of pressure and this drives

the circulation (Crossley et al., 2011). Much energy is spent this way, and the human heart consumes more than 5% of our total ATP production while cardiac mass is only 0.5% of body (Brown et al., 2017). Across vertebrates, the heart is an energy-demanding organ (Hillman & Hedrick, 2015). The high work load together with the conserved building plan suggest the heart is under substantial form–function constraints.

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Vertebrate heart development is programmed by much conserved gene regulatory networks, and it includes the formation of a heart tube that undergoes a pronounced looping (Olson, 2006). Chambers develop on the outer curvature of this loop and the resultant topology of the chambers is asymmetrical in all three principal anatomical planes (Moorman & Christoffels, 2003). The asymmetry is thought to facilitate streaming of blood (Kilner et al., 2000). Some parameters relating cardiac function can be similar within clades and in mammals, for example, the systemic mean arterial pressure is essentially similar (Poulsen et al., 2018). It is then interesting to observe that the left ventricle, which delivers this pressure, can vary quite some in morphology (Rowlatt, 1990). The greatest variation in form and function of the heart in any vertebrate class, is in bony fish (Farrell, 2023). While tunas are often highlighted as extreme cases that reveal general rules (Farrell & Smith, 2017), there are then many exceptions to these rules, and it is often the case that organismal activity levels and ecological niches are poor predictors of cardiac morphology (Icardo, 2017). Within our literature, there is then a tension between on the one hand what we know of form and function, revealed as the conservation between hearts, and on the other hand, the diversity in form and function which questions whether we understand the form–function relations of the heart. Cases of extreme anatomy are interesting in this context, because they can be particularly overt tests of our understanding.

Descriptions of the internal anatomy of the sunfishes have a long history that include occasional mentions of the heart (Cleveland, 1862; Cuvier, 1835; Gregory & Raven, 1934; Plami, 1773). A previously published image of the internal anatomy of the heart of the Ocean sunfish (*Mola mola*, Molidae, Chanet et al., 2012) suggests the presence of a topology to the cardiac chambers that is simpler than in any known adult vertebrate. Such simple topology would challenge the notion that a vertebrate heart must have a pronounced asymmetry to function normally. Here, we describe the gross morphology of the sunfish heart based on nondestructive imaging of three specimens, one of which is the specimen from (Chanet et al., 2012), supplemented by nondestructive naked-eye observations on four museum specimens.

2 | MATERIALS AND METHODS

2.1 | Specimens

From Chanet et al. (2012), we were kindly provided with the full MRI dataset of the single large sunfish they investigated. A second specimen, a relatively small sunfish of 7 kg, was investigated on the basis of a CT scan that was made to assess the mineral density of fish skeletons (Lauridsen et al., 2022). The third specimen that was investigated in detail came from Naturalis Biodiversity Center, Leiden, The Netherlands, with specimen code RMNH.PISC.84920. This was from a beached fish with an estimated mass of 380 kg. Additional four museum specimens were investigated by nondestructive naked-eye observations only; one specimen labeled as *Orthogoriscus*

mola 438^a from Museum Vrolik (Amsterdam UMC, The Netherlands), and three specimens from Naturalis Biodiversity Center labeled on jar as *Orthogoriscus mola* with specimen codes RMNH.PISC.86921, RMNH.PISC.86919, and RMNH.PISC.86920.

To investigate and visualize the cardiac chamber topology of various vertebrates, we made screenshots of image planes of the following media on the MorphoSource database (www.morphosource.org): 000345972 (*Plethodon cinereus*, Plethodontidae, AMNH:Herpetology:A-159522), 000346019 (*Necturus maculatus*, Proteidae, amnh:herpetology:FS-26617), 000530234 (*Diretmoides pauciradiatus*, Diretmidae, UF:Fish:233380), 000533031 (*Etmopterus bullisi*, Etmopteridae UF:Fish:108504), 000533044 (*Oncorhynchus mykiss*, Salmonidae, UF:Fish:91365), 000573782 (*Lestidium nudum*, Lestidiidae, YPM:VZ:YPM ICH 009951), 000573786 (*Chaetodon capistratus*, Chaetodontidae, YPM:VZ:YPM ICH 021755.001), 000573802 (*Embiotoca jacksoni*, Embiotocidae, YPM:VZ:YPM ICH 030191), 000574453 (*Exocoetus volitans*, Exocoetidae, UF:Fish:231939), 000576494 (*Archilochus colubris*, Trochilidae, UF:Birds:52652), 000593913 (*Caranx hippos*, Carangidae, UF:Fish:127945), 000593921 (*Capropygia unistriata*, Aracanidae, ANSP:FISH:114115), 000594282 (*Psilodracus breviceps*, Bathydraconidae, UF:Fish:82781), 000595502 (*Astrapogon stellatus*, Apogonidae, UF:Fish:181014), 000596673 (*Amia calva*, Amiidae, UF:Fish:236194), 000596798 (*Xenolepidichthys dalgleishi*, Grammicolepididae, YPM:VZ:YPM ICH 011455), 000598555 (*Trachelyichthys decaradiatus*, Auchenipteridae, UF:Fish:189530), 000600890 (*Odontophrynus americanus*, Odontophrynidae, YPM:VZ:YPM HERA 012496), 000604772 (*Gymnophthalmus speciosus*, Gymnophthalmidae, UF:Herp:188822) and 000604889 (*Acomys cahirinus*, Muridae, YPM:VZ:YPM MAM 005794). These specimens were chosen because they could serve as reference points to the previously described evolution of cardiac topology, or because they were phylogenetically close to sunfish (Santini et al., 2013), or because their body shape resembles that of sunfish. In addition, specimen were selected on good spatial resolution and good contrast of cardiac tissue relative to blood and pericardial fluid. Most specimens were imaged in the plane that best approximated the sagittal plane, while in the reptile and in the mammal specimen, the horizontal plane was chosen as it better revealed the topology of the chambers.

2.2 | MRI and reconstruction

For MRI, to wash out compounds in the preservation fluid that diminishes the tissue-free fluid contrast, the heart was placed under running tap water for 3 days. It was then immersed in a bucket with water and scanned on a 3T Ingenia clinical MRI scanner (Philips, Best, The Netherlands) using a standard 16-channel head coil. To this end, a high-resolution isotropic 3D T1-weighted gradient-echo sequence was used in order to suppress fluids for optimal contrast. Specific sequence parameters were as follows: TR/TE = 10/2.1 ms, flip angle = 20°, FOV = 300 × 300 × 150 mm, resolution = 0.7 × 0.7 × 0.7 mm³, total scan time = 11 min. We imported the image stack to the 3D software Amira (version 3D 2021.2, FEI SAS,

Thermo Fisher Scientific). A Volume Rendering was made of the data and a plane of sectioning was made using the Slice module. Next, labeling of the cardiac chambers and the atrioventricular canal was done in the Segmentation Editor module. From the label file, using the Generate Surface function, a surface file was made that was visualized using the Surface View function. This was done in the same window as the volume rendering whereby the heart model was projected into it. The conversion of the 3D model to an interactive pdf was done as previously described (de Bakker et al., 2016).

3 | RESULTS AND DISCUSSION

The topology of the heart of cartilaginous fish, which likely represents the primitive topology of the heart of jawed vertebrates (Grimes & Kirby, 2009), exhibits pronounced asymmetry; venous blood is collected in a caudo-dorsal sinus venosus, which medially leads into a cranio-dorsal atrium, which on the left leads into a caudo-ventral ventricle, the lumen of which on the right leads into a cranio-ventral outflow tract, or conus arteriosus (Figure 1a,b). When seen from the left, this topology resembles the letter S (Figure 1b). Bony fish lose much of the lateral (left–right) asymmetry during embryonic development, but the S-topology persists (Figure 1c). Accordingly, the S-topology is considered the evolutionary conserved building plan of the heart (Grimes & Kirby, 2009; Icardo & Colvee, 2011; Jensen, Wang, et al. 2013; Keith & Flack, 1907). When we inspect the clear image in the sagittal plane of the heart of the sunfish from Chanet et al. (2012), the expected S-topology is not apparent, and an older illustration of a partial heart is also consistent with the presence of an unusual cardiac topology (Plamì, 1773).

Already Goodrich (1930) noticed evolutionary trends in the position of the atrium relative to the ventricle, but cardiac topology is not a topic that attracts much attention. Even if the S-topology is evolutionary conserved, it could be a simplistic analysis to look for the S-topology in animals that have a pulmonary circulation in addition to the evolutionary older systemic circulation. For example, the caudo-dorsal sinus venosus is the beginning of the S-topology of the systemic circulation, whereas the pulmonary circulation has no chamber upstream of the left atrium (Jensen et al., 2017). Nonetheless, the S-topology of the systemic circulation is present in extant lungfish and coelacanth (Grimes & Kirby, 2009; Icardo, 2017; Klitgaard, 1978; Robertson, 1913), and it largely persists in extant salamanders (Figure 1d). Then, by inference, it was likely present in the hearts of early tetrapods. In most tetrapods, there is a further change to the S-topology as the atria become positioned further cranially (Goodrich, 1930). In these animals, there can be a quite sharp angle between the ventricular inflow, the ventricular apex, and the ventricular outflow (Figure 1). Also, while the hearts of most reptiles (including Aves) are parallel to the body long-axis, in many mammals, the cardiac long-axis is oriented to the caudal left, including humans and monotremes (Rowlatt, 1990). Nonetheless, overall, the topology of the cardiac chambers is quite consistent within the major groupings of vertebrates (Goodrich, 1930). Ray-fined fish deviate in this regard, however.

In the hearts of ray-fined fish, there is only a slight left–right asymmetry, but there is unparalleled variation along the caudo-cranial and dorso-ventral axes (Grimes & Kirby, 2009; Icardo, 2017; Santer, 1985). Also, the shape of the cardiac ventricle and the morphology of its wall varies more than in other vertebrate groups (Farrell, 2023; Icardo, 2017; Tota & Garofalo, 2012). The ventricles of ray-fined fish have been categorized as being tubular (Figure 1h), sac-like (Figure 1i), or pyramidal in shape (Santer, 1985) (please note it has been cautioned that there are many morphologies that are intermediate relative to the three categories (Icardo, 2017)). Intuitively, these shapes could relate to the shape of the body. Among reptiles and amphibians, for example, snakes and caecilians are comparatively elongate, and their hearts are caudo-cranially long (de Bakker et al., 2015). In some species of ray-fined fish, both body and heart are comparatively elongate, but in many species, only the body is elongate (Icardo, 2017). The sunfish has a quite extreme body plan, but it is not known whether the shape of its heart correlates to it. While it is very likely the case that evolutionary changes to cardiac form relates to function, it is less clear to what extent the form of the body itself can impact on the form of the heart.

A further categorization of the fish cardiac ventricle concerns the proportion of trabecular versus compact myocardium and the extent of coronary vasculature (Santer & Walker, 1980; Satchell, 1991; Tota et al., 1983). These categories have been correlated with various aspects of ventricular function and further to the extraordinary diversity among ray-fined fish in ecological niches, activity levels, phylogeny, life history and more (Farrell, 2023; Icardo, 2017; Santer, 1985). Tunas are often highlighted since the high activity levels of these apex predators correlate with high cardiac outputs and blood pressures and with a ventricle that is distinctively pyramidal and has a high proportion of compact muscle (Farrell, 2023; Tota & Garofalo, 2012). One concern is that the proportion of compact muscle may have been overestimated and, in any event, if hearts of tunas exemplify a general rule then there are many exceptions to it (Icardo, 2017). For example, cold acclimation in trout associate with increased pressure-generating capacity and a reduced proportion of compact myocardium (Keen et al., 2017). In aggregate, there are no simple and broadly accepted explanations for the variation in cardiac morphology in ray-fined fish.

One premise of the study of cardiac and especially ventricular morphology is that the reproducible observations of anatomical variation relate somehow to functionally important parameters (e.g., Santer, 1985; Farrell & Smith, 2017). In principle, however, if much variation in anatomy can deliver approximately the same function, then the anatomy can vary without a great selection pressure working against it, that is, if the anatomical variation has limited impact on organismal fitness. And perhaps the absence of much cardiac variation, as seen among birds for example, is not necessarily indicative of severe functional constraints, because mammal hearts exhibit much more anatomical variation than bird hearts, yet they perform almost at the same level (Kroneman et al., 2019). Extreme cases, such as the nearly separated left and right ventricle of the sea cows (Rowlatt, 1990), could be evidence that divergent cardiac

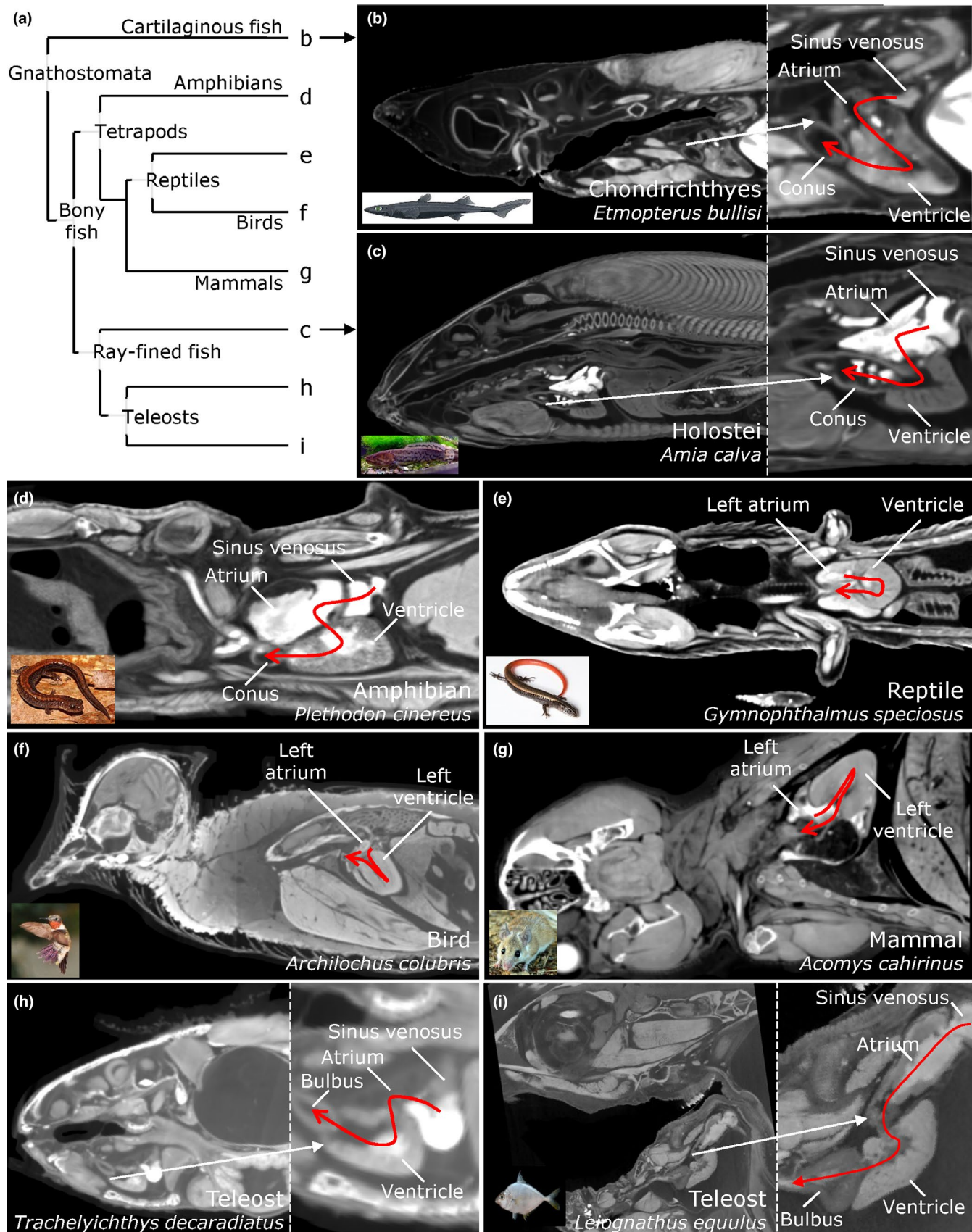


FIGURE 1 Heart topology of gnathostomes (a). Vertebrate phylogeny. (b–i) Cardiac chamber topology of various gnathostomes based on CT imaging of iodine-stained specimens, adapted from Morphosource media 000533031 (b), 000596673 (c), 000345972 (d), 000604772 (e), 000576494 (f), 000604889 (g), 000598555 (h), 000574511 (i). Inserts showing whole animals are taken from Wikipedia.

anatomies can achieve similar function. It then becomes an interesting question how divergent cardiac morphology can be and still be fully compatible with life. This question is the main motivation for this study where we expand on a previous study of the anatomy of the internal organs of the sunfish (Chanet et al., 2012) in which an image of the heart suggested to us that the cardiac topology exhibited an extremely simple loop (Figure 2a).

In Figure 2b, we show the reconstruction of various organs of a 7kg sunfish based on CT-generated images. While the cardiac chambers could be segmented relative to the pericardial fluid, the difference between chamber tissue and lumen was quite fuzzy and tissue volumes were not estimated. Valves were indistinct. The reconstruction confirmed the typical piscine position of the heart, that is, it is cranial to the liver and ventral to the buccal cavity and gills. It further corroborated the pronounced dorso-ventral elongation of

the atrium (Figure 2a,b). Such atrial morphology, together with an almost vertically oriented lumen of the bulbus arteriosus and proximal part of the ventral aorta, gives the impression that the ventricle in particular is positioned far ventrally. The central lumen of the sunfish ventricle has a gentle bend and the whole ventricle resembles a quarter of a torus. In effect, there is no morphologically distinct apex (Figure 2a,b, interactive pdfs of these two hearts are found in the Supplementary Material—Data S1). The sunfish heart, in aggregate, comprise the expected components of a teleost heart but its topology appears as a distortion from the typical S-shape toward a J-shape. While elements of sunfish heart has been described before (Cleland, 1862; Plami, 1773), there has not been, as far as we can tell, any emphasis on this unusual topology.

Sunfish belong to the order Tetraodontiformes (Santini et al., 2013) but other tetraodontiform fish such as boxfish, which

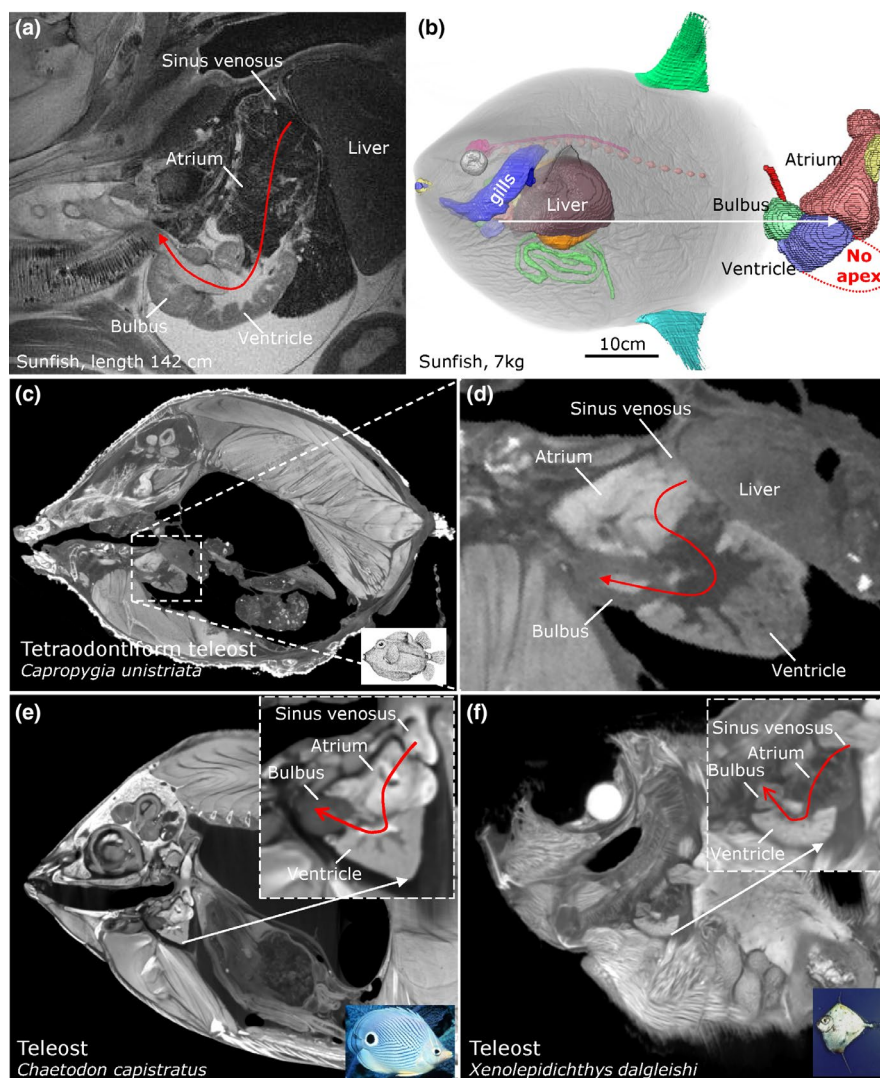


FIGURE 2 Sunfish heart shape (a). Adapted image from Chanet et al., 2012 of MRI image in the sagittal plane of a sunfish. (b). Three-dimensional reconstruction of a small sunfish and internal organs based on CT scan. (c, d). A typical piscine heart in a boxfish (Tetraodontiformes). (e, f) Cardiac chamber topology in fish with a body-form that resembles that of sunfish. (c–f) are based on CT imaging of iodine-stained specimens, adapted from Morphosource media 000593921 (d), 000573786 (e), 000596798 (f). Inserts showing whole animals are taken from Wikipedia.

is much less left-right shallow compared with sunfish, can have the typical piscine S-topology to the heart (Figure 2c,d). These observations suggest the unusual topology of the sunfish heart is related to the unusual shape of its body. To test this conjecture, we surveyed CT-image stacks of other ray-finned fish that are distinctively left-right shallow and fairly dorso-ventrally high. Subtle signs of dorso-ventral elongation of the heart could be seen in the four-eye butterflyfish (*Chaetodon capistratus*), such as a quite dorsal position of the sinus venosus, but in contrast to the sunfish the ventricle is pyramidal in shape and a distinct apex is apparent (Figure 2e). In the much dorso-ventrally elongate spotted tinselfish, the topology of the heart approximates that of the sunfish (Figure 2f); the sinus

venosus has a quite dorsal position, the atrium has a mostly dorso-ventral orientation, and the outflow tract lumen is almost vertical. The ventricle, however, quite resembles the typical piscine "sac-like" morphology and appears to have a greater bend than the quarter-torus of the sunfish ventricle (Figure 2f).

Next, we investigated the large excised heart of a stranded sunfish with an estimated body mass of 380 kg. This heart was imaged with MRI, and a simple reconstruction showed a good correspondence between the physical and the reconstructed heart (Figure 3a), and the previously described hearts (Figure 2a,b). Also, there was substantial likeness between these hearts and the four museum specimens that were assessed by nondestructive and naked-eye observations only.

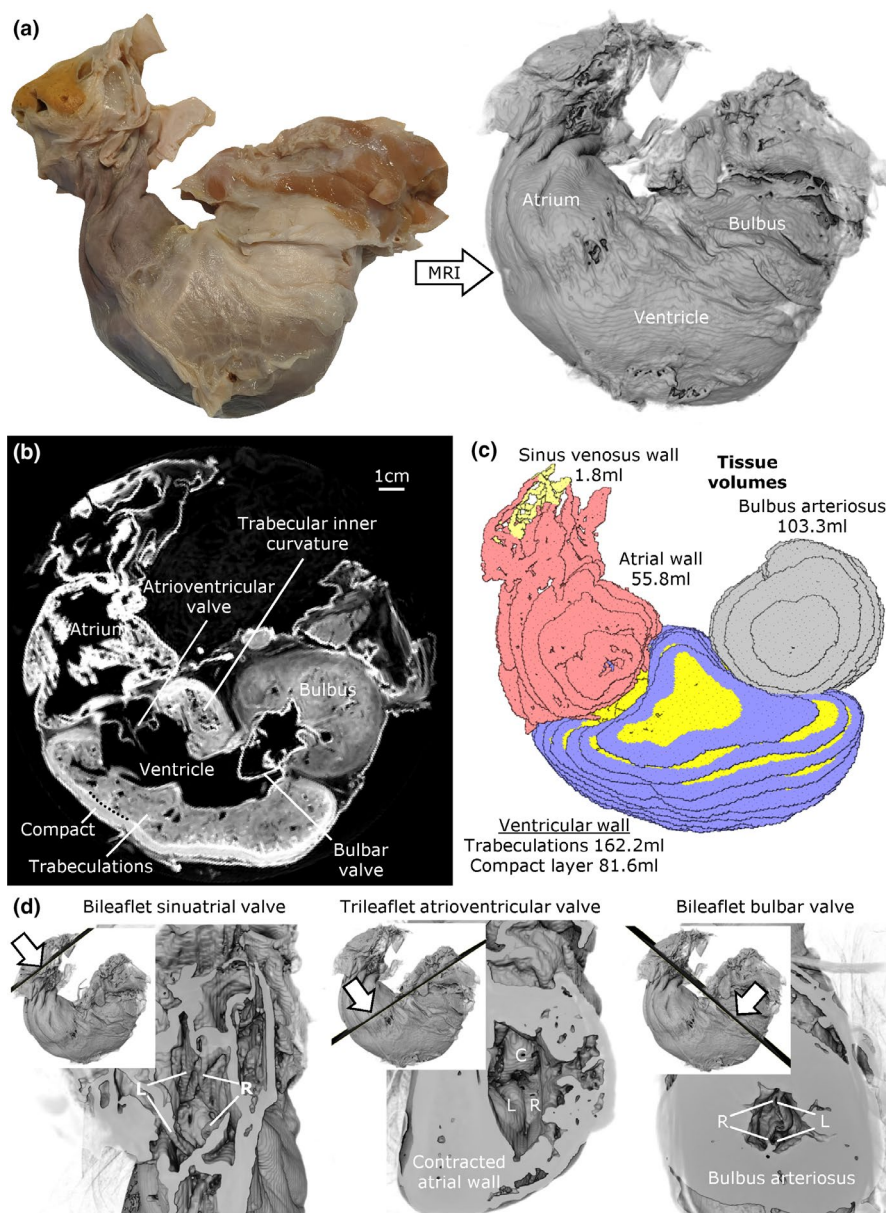


FIGURE 3 Detailed anatomical study of the heart of a large sunfish. (a). The actual and the reconstructed heart are highly similar (viewed from the right). (b) Internal anatomy of the sunfish heart, notice in the ventricle the substantial compact layer and the extensive trabeculation of the inner curvature. (c) Visualization of segmentations that were used to estimate tissue volumes. (d) Visualization of the reconstructed valves; C, cranial; L, left; R, right.

On the MRI, junctions and valves between chambers were readily visible, there was good contrast between tissue and lumen, and in the ventricle, the outer compact layer was distinct from the trabecular layer which had a relatively low signal intensity (Figure 3b). One explanation for the low signal intensity could be that the trabecular layer retained some water in the intertrabecular recesses. We then segmented these structures on every tenth image in the MRI-stack and using the principle of Cavalieri, we estimated the volume of these (Figure 3c). This yielded a total cardiac tissue volume of 301 mL, which equals a cardiac mass relative to body mass of about 0.08%, which is a value that is often found in fish (Farrell & Smith, 2017; Santer, 1985; Tota & Garofalo, 2012). In many hearts, an upstream chamber has approximately one-sixth the tissue volume of the downstream chamber (Jensen, van den Berg, et al., 2013); in the large sunfish heart, the tissue volume of the sinus venosus was small relative to the atrium (3%), but the sinus venosus varies much in size fish (Icardo, 2017; Satchell, 1991), whereas the atrial tissue volume was proportionally large to the ventricle, 23%. When a valve is present in the sinuatrial junction, it has two leaflets (Icardo, 2017), and this was also the case in the sunfish (Figure 3d), as previously described (Cleland, 1862). The atrioventricular valve is usually dominated by two leaflets (Icardo, 2017), whereas the sunfish atrioventricular valve had three approximately equally sized leaflets (Figure 3d). Three leaflets were also observed by Plami (1773), whereas Cleland, 1862 found four of which two were markedly larger. The valve of the outflow tract typically has two leaflets in teleosts (Icardo, 2017), and this was also the case in the sunfish (Figure 3d, an interactive pdfs of these structures of this heart is found in the Supplementary Material—Data S1). (1773) 1862 Valves of the sunfish heart are only illustrated here and in Chanet et al. (2012), and it is then difficult to assess whether the contradictory descriptions in the literature reflect biological variation or analytical errors.

The ventricular myocardium itself comprised 33.5% compact myocardium and 66.5% trabecular myocardium. It is likely that the volume estimate of the trabecular myocardium is somewhat inflated by the inclusion of intertrabecular recesses and if so, the proportion of compact myocardium could be greater. Either way, 33.5% compact myocardium is an intermediate-to-high value for ray-fined fish, among which two-thirds of have exclusively trabecular ventricular walls (Farrell & Smith, 2017; Icardo, 2017; Santer, 1985; Tota et al., 1983). The quantifications of compact and trabecular myocardium was pioneered by Santer and Walker (1980) who reported the absence of a compact layer in most fish including a tetraodontiform boxfish. When we analyzed our sunfish ventricle as previously (Santer & Walker, 1980), using a single transverse section that includes the atrioventricular canal, we got 33.9% compact myocardium. Similar values were reported for some species of salmon and mackerel and are almost as high as in some species of tuna (Santer & Walker, 1980). A further specialization of the sunfish ventricle may be the extent to which the inner curvature is trabeculated, as this segment appears much less developed in the boxfish (Figures 3b and 2d). The inner curvature in amniotes is transcriptionally repressed from developing (trabeculated) chamber myocardium (Jensen, Wang, et al. 2013), and very little tissue is found in this part of the

ventricle in many ray-fined fish and lungfish (Icardo, 2017) while a trabeculated inner curvature is not infrequent among ray-fined fish either (e.g., Figure 1i).

Taken together, the Ocean sunfish heart exhibits an extraordinary simple topology, which is likely a recent evolutionary development. The sunfish ventricle could be considered the least curved ventricle described to date for any vertebrate. A trend toward a similar topology in other fish that are left-right shallow and dorso-ventrally high suggests that the heart topology relates in part to the overall shape of the body. Such observations in conjunction with the observations of a broad heart in the broad-bodied turtles and elongate heart in the very slender snakes and caecilian amphibians (de Bakker et al., 2015) strongly suggest that cardiac form not only relates to cardiac function. Sunfish can episodically reach substantial swimming speeds (Nyegaard et al., 2023), but their daily displacement is only some 10km (Sousa et al., 2016), and perhaps the ventricular morphology relates to the comparatively low activity levels. On the other hand, the relative cardiac mass is likely typical of fish and the amount of compact myocardium is also found in fish with activity levels and aortic blood pressure that are fairly high. As has been stressed before, it is often challenging to correlate (piscine) cardiac anatomy to function (Farrell, 2023; Icardo, 2017), and the sunfish heart with its derived simplicity may provide another example of this.

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DATA AVAILABILITY STATEMENT

Image stacks and label files for 3D reconstructions that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

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