Chondrichthyan Evolution, Diversity, and Senses

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Abstract

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Chondrichthyans are one of two major clades of living jawed vertebrates, with a rich fossil record potentially extending back to the Late Ordovician (455 million years ago, mya). The main groups of chondrichthyans include the **chimaeroids**, **sharks**, and **skates** and **rays**. This chapter outlines the major events in chondrichthyan evolution, focusing on features of the **cranium**, **jaw** and jaw musculature, and **gill arch skeleton**. The "spiny sharks" (**acanthodians**) and other stem chondrichthyans have recently been shown to exhibit a mosaic of chondrichthyan and osteichthyan characters. Taxa such as **iniopterygians** and chondrenchelyiforms, resolved as stem group chimaeroids, appear in the Carboniferous and display dramatic body forms and unusual fin morphology. Chondrichthyans also show a considerable range of **dentitions**, both in terms of morphology and development, particularly modified in the chimaeroids. In addition to their differing tooth morphologies, chondrichthyans have several types of **jaw suspensions** to support a range of feeding and breathing modes. Sharks have well-developed brains that vary according to the environment rather than phylogeny. Their senses are also well-developed and finely tuned to best perform in their particular ecological niche. The long evolutionary history of chondrichthyans and their great diversity as well as the retention of some primitive characters make them good models for evolutionary and developmental studies.

Introduction

What Are Chondrichthyes?

Modern Chondrichthyes are jawed vertebrates lacking bones, instead possessing an internal skeleton composed of **cartilage**, with differing patterns of calcification in the vertebral centra (known as areolar) versus the rest of the skeleton, where it includes a combination of **globular** and **prismatic** calcification (Dean and Summers 2006). With respect to the latter, mineralization forms on the surface of the cartilage, in small plate-like structures known as **tesserae** (Dean et al. 2015). There are two major chondrichthyan clades, including the **Holocephali** and **Elasmobranchii**. The Elasmobranchii include sharks (**Selachii**), which include the **Galeomorphii** and **Squalomorphii**, and skates and rays (**Batoidea**), representing 96% of described modern species. By comparison, the Holocephali (**Chimaeroidei:,** chimaerids, rhinochimaerids, callorhinchids) make up the remaining 4% of modern chondrichthyans. The phylogenetic relationships of these groups are presented in Fig. 4.1.

Fig. 4.1

Phylogeny of extant chondrichthyans, showing the major groups. The base of each node shows the relative number of species in each group. Modified from Renz et al. (2013). Specimen drawings by CB

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Chondrichthyans have a rich fossil record, originating in the Ordovician period (Andreev et al. 2015, 2016). Much of this early record comprises external dermal denticles, or scales, with chondrichthyan body fossils occurring in the Lower Devonian (e.g., *Cladoselache*, *Doliodus*; Williams 2001; Miller et al. 2003). Any discussion of the chondrichthyan fossil record must also now be re-evaluated in light of recent phylogenies that resolve acanthodians as stem chondrichthyans (Brazeau 2009; Davis et al. 2012; Zhu et al. 2012; Brazeau and Friedman 2015; Coates et al. 2017). Acanthodians are often referred to as "spiny sharks," with small scales and spines in front of the paired and unpaired fins. New fossils from the MOTH fauna in northern Canada included taxa with acanthodian characteristics such as these fin spines but with scales that were more chondrichthyan-like (Hanke and Wilson 2010). Following this, a variety of phylogenetic analyses resolved certain acanthodians as stem chondrichthyans, with Zhu et al. (2012) producing the first analysis of jawed fishes that placed all acanthodians on this stem (see Fig. 2.1 in Chap. 2 and Fig. 4.2, purple and lilac).

Fig. 4.2

Phylogeny of chondrichthyans showing the approximate time of first appearance of body fossils and extinction. Scales and spines of chondrichthyans and "acanthodians" are known from the Ordovician and Silurian and are illustrated by scales and fin at the base of the phylogeny. Topology and origination and extinction dates from Coates et al. (2018) and references in the text. Batoid and Selachimorpha split from Aschliman et al. (2012). All specimen drawings by CAB. **Black:** Osteichthyes, actinopterygians represented by a sturgeon and sarcopterygian by a coelacanth. **Purple:** Acanthodid stem chondrichthyans represented by *Diplacanthus*. **Lilac**: Non-acanthodid stem chondrichthyans represented by *Gladbachus*. **Red**: *Doliodus*. **Dark Green**: Iniopterygians and holocephalans represented by *Rainerichthyes* and *Callorhinchus*. **Taupe**: Symmoriida represented by *Cladoselache*. **Brick red**: Paleoselachii represented by *Falcatus*. **Yellow**: Xenacanthiformes represented by *Triodus*. **Pale green**: Hybodontiformes

represented by *Tristychius*. **Dark blue**: Neoselachii represented by *Squalus*. **Aqua**: Batoidea represented by *Torpedo*. **Pale blue**: Selachimorpha represented by *Carcharias taurus*

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As jawed vertebrates, chondrichthyans have opposing upper and lower **jaws**, with the upper jaw (**palatoquadrate**) articulating or fused with the **braincase** in a variety of ways, providing jaw support. Teeth are arranged on the upper and lower jaws into functional dentitions. One characteristic of chondrichthyans is that teeth are produced, lost, and replaced in a continuous manner. This is more apparent in sharks and rays, although the **tooth plates** of the holocephalan dentition also develop from their base as the biting surface is worn away (Stahl 1999). Other characteristic chondrichthyan features include the extensive covering of small scales (e.g., Reif 1925; but not the Holocephali), which are organized along the body to improve hydrodynamic function (Reif 1978; Dean and Bhushan 2010); internal fertilization involving modifications of the male pelvic fin to transfer sperm into the female; a connection between the inner ear and the outside environment via the endolymphatic duct; a spiral-shaped intestine and lipid-filled liver to aid in buoyancy; eyes supported by an eyestalk; and a solid cartilaginous braincase supporting the sensory capsules.

Although these features characterize chondrichthyans, there are notable differences with respect to fossil taxa, for example, various fossil species possess a braincase divided by various fissures, shared with bony fishes, and teeth that are not shed and lost, but are retained in often large **tooth whorls**. In this chapter we will review chondrichthyan features more specifically related to the cranium (braincase), brain and sensory organs, jaws, and related musculature. We will also review recent advances in chondrichthyan phylogeny, the framework upon which we base our evolutionary interpretations.

Historical Overview

The cartilaginous skeleton of chondrichthyans was traditionally thought to be a primitive (plesiomorphic) feature, but two lines of evidence refute this: recent phylogenetic analyses resolve the acanthodians (spiny sharks) as stem group Chondrichthyes (Zhu et al. 2012; Coates et al. 2017). This extinct group of fishes, first appearing in the fossil record in the Ordovician period (444 mya; Karatajūtė-Talimaa and Predtechenskyj 1995; Brazeau and Friedman 2015), had a superficial bony covering over parts of the head and the front (pectoral) fins. The majority of acanthodians possess bony spines supporting each fin as noted above and often a series of spines between the paired fins (Janvier 1996), although some acanthodians lack these spines (Burrow and Young 1999; Hanke and Wilson 2010). The body is covered by small scales, while the internal skeleton is not preserved and so must have been made of unmineralized cartilage. Secondly, fossil sharks have been discovered with intermediate stages of evolution of the tessellated cartilages, a type of mineralized cartilage unique to chondrichthyans, and show it evolved from an ancestor possessing a bony skeleton (Long et al. 2015). Thus, chondrichthyans have lost the bone characteristic of the bony fishes (Actinopterygii; Ryll et al. 2014) and evolved surficial mineralization (tesserae) of their cartilaginous skeleton.

The concept of the great nineteenth-century anatomists of an ordered, linear progression of vertebrate evolution from cyclostomes (e.g., hagfish) to sharks and rays to bony fish and thence to tetrapods has dominated zoological thought and teaching ever since, and sharks had a key place in this progression, so much so that a skeptic among the classical anatomists coined the term "elasmobranch worship" (see Gee 2007). More recently this orderly sequence has been challenged

with new fossil finds, particularly from the Silurian of China (Zhu et al. 2012, Zhu et al. 2013) indicating extant chondrichthyans and osteichthyans exhibiting a mosaic of ancestral and derived characters. Nevertheless, elasmobranchs in particular do retain some primitive features not found in other extant fish, particularly in comparison with modern bony fish—notably in their skull, cardiovascular system, sensory organs, and fin structure—and are thus of great importance in understanding the evolution of organ systems.

Evolutionary History of Chondrichthyans

The first indication of chondrichthyan origins are "chondrichthyan-like" scales from the Middle Ordovician of North America, China, and Mongolia (e.g., Harding Sandstone; Smith and Sansom 1997; Andreev et al. 2015), some 50 million years before body fossils are known [with respect to the **acanthodians**, this gap is approximately 30 million years between the earliest scales, noted above, and the first acanthodian body fossil in the Late Silurian (Burrow and Rudkin 2014)]. Indeed, the early evolutionary origin of the group is known primarily from scales, suggesting early sharks were not very well mineralized, making them less likely to fossilize. It remains problematic to confidently identify chondrichthyans using only scale morphology and histology (Sansom et al. 2001, 2005) due to the plesiomorphic nature of early gnathostome scales. However, the earliest confirmed monodontoid chondrichthyan order, the **Elegestolepidida** (Lower Silurian to the Lower Devonian), is known only from scales that lack enamel and basal bone osteons and possess a distinctive neck canal formation (Andreev et al. 2015). A second order of mid-Ordovician chondrichthyans, the **Mongolepidida**, recognized by their complex polyodontoid scales, is also known from North America, China, and Mongolia (Andreev et al. 2016), indicating that a chondrichthyan radiation preceded the Lower Devonian "nektonic revolution" (sensu Klug et al. 2010).

Acanthodians first evolve in the Ordovician period, including body fossils, although these are often scales and spines with little other morphology preserved. Taxa now resolved as stem chondrichthyans (Fig. 4.2, purple and lilac; Coates et al. 2017) which are known from more than isolated scales include taxa such as *Poracanthodes*, *Acanthodes*, and *Kathemacanthus* (Miles 1973; Gagnier and Wilson 1996; Hanke and Wilson 2010), in addition to taxa that were previously recognized as "conventionally defined" chondrichthyans (Zhu et al. 2013), e.g., *Doliodus* (Lower Devonian; Miller et al. 2003; Maisey et al. 2009), *Pucapampella*, and *Gladbachus* (Middle Devonian; Janvier and Suarez-Riglos 1986; Heidtke and Krätschmer 2001; Maisey and Anderson 2001; Coates et al. 2018). These taxa have prismatic calcified cartilage, as a component of their skeleton, which is a diagnostic feature of chondrichthyans; by comparison, the primitive gnathostome endoskeleton comprises a core of globular cartilage surrounded by **perichondral bone** (Janvier 1996; Ørvig 1951). The endoskeleton of the early Devonian chondrichthyan *Gogoselachus* has endoskeletal elements comprising layers of **nonprismatic subpolygonal tesserae** which represent a transitional condition between globular calcified cartilage and prismatic calcified cartilage (Long et al. 2015).

Doliodus problematicus is recognized to possess a mosaic of acanthodian and shark characters (Fig. 4.2, red; Maisey et al. 2017). The squamation is shark-like, as is the dentition, braincase, jaws, and skeleton comprising prismatic cartilage (Maisey et al. 2014). However, paired pre-pectoral, pectoral, pre-pelvic, and pelvic **fin spines** are preserved along the body, which is a characteristic of acanthodians (Maisey et al. 2009, 2017). The presence of pectoral fin spines has been argued for *Antarctilamna*, another early Devonian chondrichthyan (Miller et al. 2003; Wilson et al. 2007; Gess and Coates 2015), which, along with the presence of fin spines in some placoderms and osteichthyans (Zhu et al. 2009), indicates that paired pectoral fin spines are a gnathostome synapomorphy. *Pucapampella* has a **ventral cranial fissure** (Janvier and Suarez-Riglos 1986; Maisey 2001; Maisey and Anderson 2001; Maisey et al. 2009) which used to be a diagnostic feature for early osteichthyans and acanthodians (*Acanthodes*) but is now understood to

be a shared characteristic of all crown group gnathostomes (Brazeau and Friedman 2015; absent in placoderms). Although **Gladbachus** (Fig. 4.2, lilac and reconstruction) is one of the more complete stem chondrichthyans known (Burrow and Turner 2013*5*; Coates et al. 2018), its phylogenetic position has been problematic (Coates 2005) due to the scale morphology and histology being plesiomorphic for gnathostomes (Burrow and Turner 2013). *Gladbachus* possesses teeth (Coates et al. 2018); otherwise the earliest teeth confirmed from chondrichthyans are from the Lower Devonian taxon *Leonodus* (Mader 1986).

Many other Early and Middle Devonian taxa are known only from isolated teeth (e.g., *Aztecodus*, *Celtiberina*, *Mcmurdodus*, *Portalodus*), which show a greater diversity in crown and base shape than in Late Paleozoic taxa (Ginter et al. 2010). However, in light of the combination of characters found in **Doliodus** which led to the description that it possessed an elasmobranch-like head and an acanthodian-like body (Maisey et al. 2017), many of the taxa established on the basis of tooth morphology alone may in fact represent stem chondrichthyans. The wide diversity of tooth morphology and the global distribution of many taxa do indicate that a diversification occurred in the Givetian (Ivanov et al. 2011). The age of the chondrichthyan crown group can be resolved to the Late Devonian, based on the appearance of taxa currently identified as stem group holocephalans, including those known from more complete specimens such as *Cladoselache* (Dean 1894), along with a variety of taxa based on teeth (Darras et al. 2008). Late Devonian elasmobranchs are also known from teeth (Ivanov et al. 2011) and fin spines (*Ctenacanthus*, Maisey 1984), but also braincases (*Cladodoides*, Maisey 2005), or some combination of these (*Tamiobatis*, Williams 1998).

By comparison, crown Elasmobranchii evolve much later, in the Mesozoic (Jurassic, Cretaceous, Maisey 2012; Janvier and Pradel 2015), while crown holocephalans also appear in the Mesozoic, but in the Triassic (Fig. 4.2; Stahl 1999; Janvier and Pradel 2015).

Early Origin of Holocephalans and Iniopterygians

Holocephalans or chimaeroids—elephant sharks, ratfish, or rabbitfish—originated in the Middle–Late Devonian (Darras et al. 2008; Janvier and Pradel 2015; Coates et al. 2017) and, as indicated by faunas such as Bear Gulch, Montana, were very morphologically diverse during the following period, the Carboniferous (Fig. 4.2, dark green; e.g., Stahl 1999; Grogan and Lund 2004; Lund and Grogan 2004). As mentioned above, the holocephalan crown group evolved in the Mesozoic, including callorhynchids (Jurassic), chimaeroids (Cretaceous), and rhinochimaerids (Triassic) (Stahl 1999; Janvier and Pradel 2015: Fig. 1.2). The composition of the holocephalan stem group has been changeable, with taxa such as *Cladoselache* and the Symmoriiformes (e.g., *Akmonistion*, *Cobelodus*) either resolved to the chondrichthyan stem (Pradel et al. 2011) or to the holocephalan stem (Coates and Sequeira 2001; Coates et al. 2017). The Iniopterygia has a more stable relationship as stem group holocephalans. The iniopterygians were an unusual and highly specialized group of stem group holocephalans, known only from a small number of genera, but with a range of body forms (Zangerl and Case 1973; Grogan and Lund 2009). All had stout pectoral fin projecting high up on the shoulder girdle (a synapomorphy of the group, Stahl 1980; Grogan and Lund 2009) with large pectoral spines. There are two families, the Iniopterygidae with upper jaws not fused to the braincase (**non-hyostylic**) and the Sibyrhynchidae, showing the hyostylic or **autostylic** condition (Zangerl and Case 1973; Stahl 1980; Pradel et al. 2010).

A new fossil from the Early Permian of the Karoo sandstone in South Africa, *Dwykaselachus*, has external anatomy of a group known as the Symmoriiformes (Fig. 4.2, taupe) but also chimaeroid specializations like the otic labyrinth arrangement and brain space configuration relative to large orbits (a potential adaptation to deepwater environments, a niche occupied by various holocephalans), showing a transitional phase to the characteristic chimaeroid cranium (Coates et

al. 2017). Phylogenetic analyses establish the importance of the shared similarities between *Dwykaselachus* and chimaeroids, recovering Symmoriiformes as a stem holocephalan, sister clade to the iniopterygians and holocephalans. Notably, the Late Devonian taxon *Cladoselache* is resolved phylogenetically as a symmoriid, which implies a minimum age for the elasmobranch-holocephalan split within the Devonian (Coates et al. 2017).

Major Events in the Evolution of Chondrichthyans

Chondrichthyes and Osteichthyes are referred to as crown group Gnathostomata, but importantly, there are a range of fossil jawed vertebrates that are more closely related to this crown group than are jawless vertebrates. Therefore, any consideration of the evolution of major chondrichthyan characters needs to take these taxa into account, including the placoderms (covered in the Chap. 2), which are generally characterized by having the head and the anterior part of the body covered with thin bony plates, as well as *Ramirosuarezia* (Pradel et al. 2009a, b), which is resolved as phylogenetically closer to the crown group than the placoderms (including *Entelognathus* and *Qilinyu*; Zhu et al. 2013, Zhu et al. 2016). Important features that we discuss below are related to the skull, jaws, musculature, and gill arches, which are of particular interest because they are related to feeding, breathing, and the ability to sense the surrounding environment.

An additional consideration when discussing chondrichthyan evolution is the effects of major extinctions on the group. For example, the Late Devonian saw two extinctions, the later one associated with the disappearance of the placoderms and most acanthodians, presenting a major evolutionary opportunity for both chondrichthyans and osteichthyans. Most chondrichthyans evolving in the Carboniferous possessed flatter, presumably crushing dentitions (Sallan and Coates 2010; Sallan et al. 2011), including the wide diversity of holocephalans just mentioned (Grogan and Lund 2004; Lund and Grogan 2004). Many of these taxa were affected by later extinctions in the Permian, where 96% of marine life was lost (Sepkoski 1984), although others appear to have become extinct earlier in the Permian or in the Late Carboniferous (Friedman and Sallan 2012). However, *Hybodus* and the Hybodontidae survived this extinction and are currently resolved as the sister group to living sharks and rays (Fig. 4.2, pale green). These groups, along with the chimaeroids, originated in the Mesozoic, with sharks and rays splitting in the Upper Triassic (Aschliman et al. 2012) and diversifying in the Early–Middle Jurassic (Guinot and Cavin 2015). Recent research on lamniform sharks suggests that diversity and disparity decreased shortly after the end-Cretaceous extinction (75% of marine life; Sepkoski 1984), with sharks becoming smaller and teeth becoming less robust (Belbin et al. 2017).

What Makes Them Special?

Sharks and rays are a very diverse group that occupy many different ecological niches, including both fresh and saltwater environments, and at markedly different depths. Their feeding behavior ranges from stalking predation to ambush predation to plankton filtration, with different associated locomotor patterns (Motta and Huber 2012). Their main features include a mouth on the ventral surface of the head, mobility of the upper jaw, and separate gill slits. Their jaw suspension—hinged at the back of the skull—allows the shark snout to be elevated while taking prey and the jaws to protrude toward the prey or into the seafloor in the case of rays. Separate gill slits are visible externally, usually five but also six or seven in some species (e.g., the broadnose sevengill shark *Notorynchus cepedianus*). The first gill slit is present in many species as the spiracle, a round opening on the dorsal side of the head, unlike bony fish in which the spiracle is found only in a few primitive types. Both inflow and outflow can occur via the spiracle. In rays, where the mouth is often directly in contact with the seafloor, the spiracle is particularly used for ventilation, as clean water can be taken in, rather than sand or mud (Summers and Ferry-Graham 2001). Some sharks need constant movement to force water over the gill surfaces, known as **ram ventilation**, while others can remain stationary and use suction from expansion of the mouth and

pharynx to draw water in and over the gills. Feeding is similarly achieved by "ram" and "suction" methods in different groups of sharks (Wilga and Ferry 2016). Multiple rows of large sharp teeth are characteristic of large carnivorous sharks, but many other arrangements for biting, holding, and tearing smaller prey are found. Whale and basking sharks have large numbers of tiny teeth and depend on filtering plankton at the internal openings of the gills. Rays typically have hard tooth plates for crushing crustaceans and mollusks, although manta rays are **filter feeders**. Megamouth sharks, a very large deepwater filter feeder only discovered in 1976 (*Megachasma pelagios*), has bioluminescent tissue within the mouth to attract prey.

The holocephalans are unusual compared to the sharks and rays but share with them, for example, a superficially mineralized cartilaginous skeleton and claspers. Holocephalans are typically deepwater dwellers that feed along the bottom of the ocean. They have hard, mineralized tooth plates for crushing hard-bodied prey (Huber et al. 2008; Boisvert et al. 2015). The upper jaw (palatoquadrate) suspension involves fusion to the base of the skull (**holostylic** jaw suspension); however as noted above, some Iniopterygia are non-holostylic, as are the symmoriiforms (*Cladoselache*, *Akmonistion*, and *Cobelodus*; Coates and Sequeira 2001; Maisey 2007), unlike the upper jaw attachment at two points on the cranium (amphistylic suspension) of primitive chondrichthyans or the single-point suspension of modern sharks and rays (**hyostylic**). Other key holocephalan features include an **operculum**, a flap-like covering over the external gill openings, similar to that present (but nonhomologous) in bony fish but absent in sharks, rays, and Symmoriiformes, gill arches positioned under the cranium, and a cranial clasper, which is a hook-like structure on top of the head of males of certain holocephalan taxa (but absent in Symmoriiformes) that is used to grip the pectoral fins of females during copulation, an adaptation for internal fertilization. Also, holocephalans generally lack scales, although sensory canals are lined with small, calcified rings, and embryos of taxa like *Callorhinchus milii* have rows of scales on the head that are lost during development (CB pers. obs.).

The Chondrichthyan Cranium

All craniates—animals with brains—have a cartilaginous braincase or **chondrocranium** during development, surrounding the brain (often open dorsally) and incorporating the cartilaginous supports or capsules of the eyes, inner ears, and nasal structures. In animals with bones, the osteichthyans, the chondrocranium becomes replaced by bone and covered by the bones of the outer skull. The persisting cartilaginous skull of chondrichthyans was, until quite recently, thought to be a primitive state. However, stem gnathostomes such as the placoderms had comparable outer bony plates, if not all of the chondrocranium ossified, so an entirely cartilaginous braincase is derived (Brazeau 2008). New fossils of early osteichthyans and chondrichthyans are emerging, and details of their cranial structure are used to understand the evolution of early gnathostomes.

Chondrichthyan Jaws and Jaw Suspension

As noted above, chondrichthyans are characterized by a range of types of jaw suspension, involving the attachment of the upper jaw (palatoquadrate) to the braincase or cranium (Maisey 1980, 2008) and the degree of support provided by the hyoid arch just posterior to the jaws, which includes the **hyomandibula** dorsally and the **ceratohyal** ventrally (Fig. 4.3). Although the hyomandibula provides support to the jaws, the ceratohyal forms an important part of the gill arch basket, relevant to suction feeding and how aerated water is drawn into the mouth and over the gills (suction versus ram). In sharks, the **palatoquadrate** can attach at a variety of points anteroposteriorly along the cranium (Maisey 1980: Figure 1; Wilga 2005: Figure 1), for example, on the postorbital process, and also more anteriorly, near the nasal capsules (ethmoid region). Several shark taxa also have a prominent orbital process of the palatoquadrate, including the Squalomorphii ("orbitostylic sharks," Maisey 1980: Figure 4). These attachments can be at articular surfaces or ligamentous (Wilga 2005). The hyomandibular plays a role in jaw suspension

and is relatively large, articulating to the otic region of the braincase (Maisey 1980). In skates and rays (Batoidea), palatoquadrate articulations are absent, with jaw support provided only by the hyomandibular. The batoid palatoquadrates are also shorter and do not extend anteriorly to the ethmoid region of the braincase. Among sharks, this is also the case in the galeomorphs and squalomorphs apart from *Chlamydoselachus* and hexanchoids (Lane and Maisey 2012).

Fig. 4.3

Cranial and branchial anatomy of the school shark *Galeorhinus galeus*. (**a**) Cranial and branchial skeleton, schematic. Note the upper jaw (palatoquadrate cartilage) attached to the cranium ("suspension") by the hyomandibula (second branchial arch); there is a loose sliding articulation at the orbital process (hyostylic jaw suspension). (**b**) Locations of cranial and branchial muscles (after Hughes and Ballantijn 1965; Mikoleit 2004)

With respect to stem chondrichthyans, jaws and jaw suspension are only known from *Acanthodes bronni* among the "acanthodians" (Miles 1973; Davis et al. 2012; Brazeau and de Winter 2015). Miles (1973) identified characters, including the position of the hyomandibula relative to the jugular vein that suggested a more osteichthyan-like condition. In previous phylogenetic analyses of the jawed vertebrates, the Acanthodii was resolved as a paraphyletic group, with *Acanthodes* resolved as more closely related to bony fishes, while other acanthodians were more closely related to the chondrichthyans (Brazeau 2009). Subsequent examination of the *Acanthodes* material demonstrated that the palatoquadrate articulated with the postorbital process, as in the stem chondrichthyans discussed below. The hyomandibula was thought to articulate on the otic region, another chondrichthyan character (Davis et al. 2012). Despite this, the analysis of Davis et al. (2012) resolved all acanthodians to the osteichthyan stem, contrary to Brazeau (2009). Later analyses, though, assigned acanthodians to the chondrichthyan stem, a largely stable result to this day (Zhu et al. 2013; Coates et al. 2017, 2018) (Fig. 4.2, purple and lilac). As well, Brazeau and de Winter (2015) confirmed that the hyomandibular position relative to the jugular groove was more similar to the chondrichthyan condition. Therefore, *Acanthodes* could act as a proxy for the acanthodian braincase, jaws, and jaw suspension and an outgroup condition for jaw suspension the rest of the chondrichthyan (non-acanthodian) lineage.

More phylogenetically derived stem group elasmobranchs and holocephalans generally have an elongate, cleaver-shaped palatoquadrate, including cladoselachians, *Cobelodus*, symmoriids, xenacanths, and ctenacanths, with the large flange located posterior to the orbit and articulating with the posterior margin of the postorbital process of the cranium (Maisey 1980; Lane and Maisey 2012). The jaw joint is posterior to the otic region of the braincase (Lane and Maisey 2012). An ethmoidal articulation is present, considered plesiomorphic for chondrichthyans along with the articulation to the postorbital process (Maisey 2008; Lane and Maisey 2012). Jaw musculature has been reconstructed in cladoselachians (Late Devonian; Maisey 1989) and *Cobelodus* (Maisey 2007).

The **Hybodontoidae** (Devonian to Miocene; Fig. 4.2, pale green) represent the sister group to extant sharks and rays, with their jaw suspension being recently reviewed by Lane and Maisey (2012). In many hybodont taxa, the palatoquadrate articulates anteriorly but not to the postorbital process, with a suspensory hyomandibular. Among extant sharks, this also characterizes the heterodontiforms, lamniforms (ligamentous), and the carcharhiniforms (articular facet; see also Wilga 2005).

Chondrichthyan Dentitions

Chondrichthyan dentitions are enormously varied, with the flatter, pavement-like dentitions of the skates and rays (e.g., Underwood et al. 2015) and the crushing tooth plates of the chimaeroids (Patterson 1965; Didier 1995; Stahl 1999), along with the range of dentitions in the shark, from the very small teeth in the filter-feeding basking shark (*Cetorhinus*) to the functional row of cutting blade dentitions in taxa such as the cookiecutter shark (*Isistius*; Underwood et al. 2016) to taxa with different teeth within their dentitions, such as the Port Jackson shark *Heterodontus*.

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One major feature of the chondrichthyan dentition is the ongoing **regeneration** and replacement of teeth, which develop along the base of the jaw in a structure known as the **dental lamina**, and the organization or patterning of teeth along the jaw. Recent research has provided considerable insight into the genetic network involved in the development of chondrichthyan teeth and dentitions, focused on the catshark *Scyliorhinus* (Fraser et al. 2009, 2010; Smith et al. 2009; Debiais-Thibaud et al. 2011; Fraser and Smith 2011), and links to the external dermal denticles (Fraser et al. 2010). Most recently, focus has been on shark tooth regeneration and replacement and the role played by stem cells (Rasch et al. 2016; Martin et al. 2016). The first teeth develop in more superficial epithelium along the jaw, known as the odontogenic band (Smith et al. 2009, 2016). Intriguingly, this band is associated with taste buds in the mouth, to form an odonto-gustatory band (Rasch et al. 2016). Several gene families are expressed within this band, including *Hh*, *Wnt/β-catenin*, *Bmp*, *Pitx2*, and *Fgf*, important in tooth development in bony fishes (Fraser et al. 2006, 2012), suggesting a very deep evolutionary history. These gene families are also important in all stages of tooth regeneration within the dental lamina.

As the epithelial cells of the odonto-gustatory band proliferate, the dental lamina begins to develop, with cells expressing *β-catenin*, *Pitx1*, and *Sox2* (Rasch et al. 2016). Stem cells are held within the dental lamina (successional lamina) but, also more superficially, within taste buds proximate to the oral epithelium (Rasch et al. 2016). The genes *β-catenin*, *Pitx1*, and *Lef1* are expressed in conjunction with regenerating teeth, but not *shh*, which is only involved in tooth initiation.

Musculature

Muscles for Jaw Mechanics

Filter feeders aside, chondrichthyans use their jaws to bite, crush, or grasp their prey, with tooth shapes and sizes appropriate to these mechanisms. The jaws are developmentally separate to the rest of the skull, which houses the brain and sensory organs: the upper and lower jaws are developed from the first and second pharyngeal arches, a series of developmental structures that form jaws anteriorly and branchial arches posteriorly (origin of jaws covered in Chap. 2, but see also Chaps. 1 and 3). Branchial arches are skeletally supported arches that typically have openings between them, forming the gill slits. The jaws have an outer layer of mineralized (calcified) cartilage arranged in tiles over a non-mineralized core. This arrangement allows considerable force to be applied. In sharks and rays, two sets of muscles are used, one to protrude the upper jaw and the other to close the lower jaw against the upper (Fig. 4.4). Upper jaw protrusion by the **m. preorbitalis** (Fig. 4.4) is most obvious in large predatory sharks, which elevate the snout to allow the protruded jaw mechanism a more front-on approach to the prey. The jaw is closed by the **m. adductor mandibulae**, which can have several portions (see Ziermann et al. 2017).

Fig. 4.4

External and muscular anatomy of the head of the school shark *Galeorhinus galeus.* (**a**, **b**) Lateral view; (**c**, **d**) ventral view. (**a**) External anatomy and (**b**) superficial dissection to show jaw muscles. (**c**) External anatomy and (**d**) superficial dissection to show jaw adductors (adductor mandibulae, preorbitalis) and depressor (coracomandibularis). Abbreviations: levator a.p., levator arcus palatini; adductor a.p., adductor arcus palatine

Modification of the Jaw Musculature in Suction Feeders

Rays have developed a very mobile jaw mechanism that can be hinged ventrally to the body to extend into the substrate (seafloor) to take prey by biting or suction. The arrangement of muscle fibers in the jaw-closing muscle is effective at maximizing force or speed of closure, varying among different feeding patterns in diverse sharks. In fact, the jaw-closing muscles of sharks are mechanically more effective than those of mammals, which evolved many millions of years later.

Jaw Musculature in Prey Crushers

Holocephalans have the upper jaw fused along the base of the skull and cannot protrude the upper jaw; these fish have a complex pattern of muscles in the snout including the **m. levator anguli oris**, **m. labialis,** and **m. prelabialis** which are labial muscles, in addition to the **m. preorbitalis** found in elasmobranchs. Holocephalan snout muscles have been attempted to be homologized to the labial muscles of cyclostomes and the m. preorbitalis of elasmobranchs (Ziermann et al. 2014), but as seen in the previous chapter (Chap. 2), the labial muscles of cyclostomes are unlikely to be homologous to those of chondrichthyans. Homologizing all the labial muscles of holocephalans to only the m. preorbitalis of elasmobranchs may be an oversimplification as the complex labial musculature of holocephalans appears unrelated to jaw mechanics and probably is related to movements of the sensory apparatus concentrated in the snout.

Musculature Used for Breathing, and Spiracular Breathing ers

The other important muscle function in the head is that of expansion and contraction of the pharynx and gill chambers, for the mechanics of ventilation and suction feeding. Some sharks are "obligate ram ventilators" and need to be moving all the time to have a flow of water over the gills, and other slow-moving or largely stationary species use **suction ventilation** entirely, but most chondrichthyans use a combination of ram and suction ventilation (Brainerd and Ferry-Graham 2006). To generate suction, the gill chamber (pharynx) and to a lesser extent the mouth cavity need to expand rapidly. This is accomplished by the hinged nature of the branchial skeleton, which allows changes in volume of the enclosed chamber as the hinges are operated by muscles that mainly pull the floor of the mouth and pharynx downward (Wilga and Ferry 2016). These muscles originate from the pectoral (shoulder) girdle and are the **coracomandibularis** that inserts onto the mandible and the **coracobranchialis** that inserts onto the branchial arches (Fig. 4.3).

Lateral expansion is also possible in some species, depending on the orientation of the hinges, and is assisted by sheets of muscle that surround the gill chambers. Externally there is a valve mechanism to allow an effective pump with negative pressure being generated within the gill chambers and mouth—in sharks and rays, there are soft tissue valves over each of the separate gill slits, preventing water from entering but allowing escape during the compression part of the pump cycle. In holocephalans, the gill slits are covered externally by the operculum, and these fishes are

similar to bony fishes, lungfish, and coelacanths in this respect. The operculum forms a flap valve over all the external gill openings and appears to assist suction ventilation and feeding in the way that the individual gill slits do in sharks, although the evidence in holocephalans is uncertain.

Gill Arch Evolution

As noted above, chondrichthyans have 5–7 gill arches posterior to the hyoid arch. Each jointed arch is formed from a number of dorsal (**pharyngo-** and **epibranchials**) and more ventral arch elements (**hypo-** and **ceratobranchials**) that articulate with a ventral midline series of **basibranchials**, forming a highly flexible unit with associated musculature (Miyake et al. 1992; Mallatt 1997; Wilga et al. 2001) to not only bring food into the oral cavity but aerated water as well. The arrangement of these arches has been reviewed by Nelson (1969), including denticles on the oropharyngeal arch surface. The general structure of the gill arches is conserved through jawed fishes, including the acanthodians (Miles 1964) and more phylogenetically basal placoderms (Carr et al. 2009; Stensiö 1963), recently reviewed by Pradel et al. (2014: Figure 3). There are differences in the number and arrangement of these arches; for example, in chondrichthyans, the pharyngo- and hypobranchials are directed posteriorly (but anteriorly in chimaeroids), while in osteichthyans these are oriented anteriorly. In keeping with previous ideas that chondrichthyan morphologies represented the primitive condition for jawed vertebrates, it was thought that the chondrichthyan arrangement of the arches, often described as a "$\sum$," was primitive (Pradel et al. 2014). Although the ventral gill arches are known in placoderms, a full complement of gill arches is unknown for comparison to crown group gnathostomes (e.g., Carr et al. 2009; Brazeau et al. 2017).

Recently, a complete and associated series of gill arches was described in the symmoriiform *Ozarcus* (Pradel et al. 2014). These showed multiple similarities to the arches of bony fishes, rather than other chondrichthyans, including having two pharyngobranchials (infra, supra), with the infrapharyngobranchials and more ventral hypobranchials having an anterior orientation, rather than posterior. As well, the last three ceratobranchials articulated to the posteriormost basibranchial, while in chondrichthyans, only the last ceratobranchial articulates with this basibranchial. When *Ozarcus* was first described, the symmoriiforms were considered to be stem group chondrichthyans (Pradel et al. 2011), and therefore the gill arches, and their similarity to bony fishes, were highly relevant to the evolution of chondrichthyan arches. However, symmoriiforms, including *Ozarcus*, are most recently resolved as stem group holocephalans (Coates et al. 2017). Important in this regard are the stem group chondrichthyans *Doliodus* and *Gladbachus*. Although branchial arches are present in *Doliodus* (Fig. 4.2, red), hypo- and pharyngobranchials were not described (Miller et al. 1993). In *Gladbachus* (Fig. 4.2, lilac), the pharyngobranchials are oriented anteriorly, the bony fish condition (Coates et al. 2017). The retention of this state in the holocephalan stem in *Ozarcus* suggests that the posterior orientation of the pharyngobranchials was attained independently in crown group holocephalans and elasmobranchs.

Chondrichthyan Brains and Senses

Among the chondrichthyans, sharks are legendary for their sensory abilities. For example, we have all heard that sharks can smell a single drop of blood in the ocean, and movies have often exaggerated the sensory abilities of sharks. This section is an overview of the **brains** and **senses** of sharks, batoids, and holocephalans, keeping in mind that sensory abilities, brain size, and organization differ greatly between species and are highly associated with a given species' ecological niche (Yopak et al. 2007). Overall, chondrichthyans have large brains relative to body size when compared with other vertebrates, and galeomorph sharks and myliobatiform rays have similar brain/body ratios to those found in mammals (Bauchot et al. 1976; Northcutt 1978; Yopak

et al. 2010). Phylogenetically more basal groups tend to have a smaller brain/body ratio, while brain size and cerebellar complexity (including foliation or folding) increase from phylogenetically more basal squalomorph sharks to more derived galeomorphs such as Carcharhinidae and Lamnidae (see phylogeny in Fig. 4.1; Yopak et al. 2007). Hammerhead sharks have the relatively largest brains, whereas whale sharks and the great white and gray nurse sharks have among the smallest brains relative to body size (Yopak et al. 2007; Yopak and Frank 2009). A similar pattern is found in batoids, with rajiforms, rhinopristiforms, and torpediniforms having smaller, less structurally complex brains than myliobatiforms (Northcutt 1978; Lisney et al. 2008). Among the rays, devil rays appear to have the largest and most complex brains (Lisney et al. 2008; Ari 2011; Yopak 2012). The brains of holocephalans are generally similar in size (and morphology) to those found in squalomorph sharks (Northcutt 1978; Yopak and Montgomery 2008). However, there is more to the brain than simply its size. Building on the pioneering work of Northcutt (1978), Yopak et al. (2007, 2009, 2010) and Lisney et al. (2008) have assessed chondrichthyan brains to evaluate the proportions of the different parts of the brain (Fig. 4.5) relative to each other and the degree to which the cerebellum is foliated. The five major brain areas are the forebrain, composed of the (1) **telencephalon** (Fig. 4.5b, pink), which as well as receiving primary **olfactory** input from the olfactory bulbs also receives multisensory input from the other modalities and is involved with multisensory processing and higher cognitive functions, and (2) the **diencephalon** (Fig. 4.5b, yellow), a multisensory relay center that acts as an interface between the brain and the endocrine systems and which plays an important role in homeostasis; (3) the midbrain or **mesencephalon** (Fig. 4.5c, blue), which is characterized by two prominent dorsal lobes, the optic tectum, which receives the majority of visual input from the retina (as well as input from other sensory modalities); and (4) the **hindbrain** (Fig. 4.5b, green), composed of the **medulla** and (5) the **cerebellum** (Fig. 4.5a). The medulla receives primary sensory input from the **octavolateralis** systems (acoustic, electroreceptive, and lateral line systems), while the cerebellum is a multimodal integration center that is important in muscle coordination and monitors the body's position in space. In some species, the cerebellum is **foliated**, which increases the surface area of the brain and is believed to increase cognitive ability as the cerebellum is involved in the integration of different stimuli (Walker and Homberger 1992; Demski and Northcutt 1996; Yopak 2012). Cerebellar foliation is phylogenetically relevant, with more basal elasmobranchs lacking foliation, holocephalans having a low **foliation index** while galeomorph sharks such as hammerheads and myliobatiform rays such as manta rays having high foliation indices (Yopak et al. 2007; Lisney et al. 2008) (see Fig. 4.1 for phylogeny). However, foliation is not entirely correlated with phylogeny and depends strongly on environment adaptability. Additionally, brain foliation often comes at the expense of brain size except in highly derived species such as the hammerhead.

Fig. 4.5

Dogfish brain drawing in (**a**) dorsal view, color-coded to show the major sensory areas. Red: olfactory. Blue: visual. Green: hearing. Purple: electroreception. Yellow: taste. Brown: lateral line/mechanoreceptor. Areas with several colors are multimodal centers that integrate inputs from several senses. (**b**) Ventral view showing four main areas of the brain. Pink: telencephalon. Yellow: diencephalon. Pale blue: mesencephalon. Pale green: hindbrain. Modified from House and Pansky (1960) by CB

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The species with the most foliated cerebellum are those that are migratory and which hunt very active agile prey. In terms of brain proportions, there are cerebrotypes (brain configuration types)

where species living in similar environments cluster (Yopak et al. 2007; Lisney et al. 2008). Bottom or near-bottom dwelling (demersal benthic) chondrichthyans such as batoids have an average-sized telencephalon, cerebellum, and medulla, with an enlarged mesencephalon. In contrast, holocephalans have very large cerebellums and an enlarged medulla but are below average relative to body size (Yopak et al. 2007). This suggests that holocephalans rely on electroreceptive, acoustic, and lateral line systems heavily. Demersal benthic species also have enlarged eyes, which may show a greater reliance on vision in these habitats. Wobbegongs and blind sharks are reef-associated bottom dwelling (benthic) species that have a reduced mesencephalon but enlarged medulla, the brain area that houses the primary sensory nuclei for the octavolateralis senses.

Many deepwater chondrichthyans have relatively small brains and a well-developed mesencephalon and medulla (Yopak and Montgomery 2008). This potentially reflects the fact that many of these species prey on invertebrates, are slower moving, and inhabit an environment that is largely "two dimensional" (i.e., horizontal and above rather than above, below, and horizontal). In contrast, the largest brains are found in open water species associated with coastal and especially reef habitats. This might be due to the complexity of the reef environment, where animals have to learn the spatial organization of the habitat and its inhabitants (Bauchot et al. 1977; Northcutt 1978, 1979), as well as the complex social behaviors between conspecifics (members of the same species) and other species (Kotrschal et al. 1998), for example, when schooling. In the case of the thresher shark, brain size and morphology could be linked to its unique prey-capturing behavior using the extremely elongated upper tail fin lobe (Lisney and Collin 2006). Cerebellar foliation seems to be linked to locomotor abilities and sensory motor integration (New 2001) with slow-moving species using lateral undulation having less foliated brains and fast swimmers having more foliated cerebellum. Brain size is also correlated with the mode of reproduction, with viviparous species having the largest brain, but this could be a phylogenetic signal since the most derived species are all viviparous. Brain size and organization are therefore influenced by habitat, locomotion, and phylogeny, but having a more basic brain could make the animal more adaptable (Brabrand 1985; Lammens et al. 1987; Wagner 2002).

Sense Organ Development

Chondrichthyans have six well-developed senses: **vision**, **smell (olfaction)**, **taste (gustation)**, **mechanoreception** (touch and vibration through the **lateral line system**), **hearing,** and **electroreception**. Given the variety of habitats these animals live in, there is also a great variability in these senses, but this section focuses on the generalities of how these develop and function in chondrichthyans.

One of the greatest evolutionary novelties of vertebrates are sense organs developing from **migratory neurogenic placodes** and **neural crest cells** (Lipovsek et al. 2017; see also Chap. 2). **Cranial placodes** are patches of thickened ectoderm in the embryonic head that give rise to paired organs involved in hearing, olfaction, and detecting vibrations (through the lateral line which runs across the head and onto the body), lenses of the eyes, as well as neurons connecting them to the brain (O'Neill et al. 2007). Taste buds are not placode derived, but the neurons connecting them to the brain are derived from cranial placodes (O'Neill et al. 2007). The organs of electroreception derive from the lateral line placodes (Baker et al. 2013), which are themselves derived from neural crest cells (Juarez et al. 2013).

All placodes share a common developmental origin. In the early neurula stage of the embryo (when the nervous system develops), the folding neural plate is horseshoe-shaped (see Fig. 2.2 in Chap. 2), and the anterior domain is called the preplacodal or pan-placodal domain (Baker and Bronner-Fraser 2001). This domain is defined molecularly by the expression of the homeodomain

transcription factors *Six1/2* and *Six4/5* which interact with the transcription cofactor *Eya1/2*. These genes are maintained in individual placodes, but different placodes are induced at different times during development by different tissues and molecules. The *Pax* (paired box) genes code for tissue-specific transcription factors and are upregulated later in cells fated to adopt different placodal fates (O'Neill et al. 2007): *Pax2* is expressed in the otic placode (hearing), *Pax3* in the ophthalmic placodes (vision), and *Pax6* in prospective lens and olfactory placodes (downregulated in olfactory placodes, Bhattacharyya et al. 2004). The **lateral line** and **electroreceptive ampullary organs** are linked developmentally by the expression of a novel chondrichthyan marker *Eya4*, and the lateral line ganglia initially express *Tbx3*. Overall, the expression of transcription factors underlying placode and cranial sensory ganglion development is highly conserved in all gnathostomes (O'Neill et al. 2007). The electrosensory ampullary organs are not unique to chondrichthyans, being present in larval lampreys, amphibians, and teleosts and are thought to be homologous in all non-teleosts (Baker et al. 2013), having re-evolved at least twice in teleosts.

Smell/Olfaction

Chondrichthyans rely on **olfaction** to detect prey, predators, and signal conspecifics (other sharks of the same species; Yopak et al. 2015; Theiss et al. 2009) as well as for navigation (Nosal et al. 2016) (Fig. 4.5 in red for areas of the brain and Fig. 4.6b). As the olfactory system is not connected to the respiratory system in sharks, water needs to be pumped into the nasal sacs to detect chemicals. In elasmobranchs, each nostril is divided by a flap of skin to separate incurrent from excurrent water flow (Walker and Homberger 1992) whereas, in chimaeroids, there is one pair of external nostrils but two channels diverting the water to the mouth, providing the same incurrent-excurrent flow-through system (Howard et al. 2013). In most chondrichthyans, water is pumped into the nasal sacs, but the forward motion of some continually swimming species (e.g., hexanchid sharks) may contribute to this as well (Howard et al. 2013). In order to detect the direction of the scent, the nostrils need to be well separated (Kajiura et al. 2005), and this depends on the taxa involved, with some holocephalans having closely placed nostrils but those of the Rhinochimaeridae (Bigelow and Schroeder 1953) being highly separated. When a scent is stronger in one nostril than the other, the animal will turn in that direction, following the scent trail in a zigzag pattern.

Fig. 4.6

The sensory system of chondrichthyans. Colored ellipse and rectangles on the shark drawing indicate the location of sensory organs. (**a**) Vision represented by a generalized shark eye redrawn from Lisney et al. (2012); Green: cornea. Pale orange: aqueous humor. Pale blue: iris. Dark blue: pseudocampanule, an intraocular muscle. Red: suspensory ligament. Pink: scleral cartilage. Yellow: vitreous humor. Gray: lens. Purple: retina. Brown: choroid and tapetum lucidum. Black: optic nerve. Dark green: sclera. (**b**) Linear olfactory lamella of a great white shark. (**c**) Hearing represented by the inner ear labyrinth from *Chimaera monstrosa* in lateral view. Yellow: anterior semicircular canal. Brown: endolymphatic duct. Blue: horizontal semicircular canal. Purple: lagenar macula (situated within the lagena). Red: macula neglecta. Green: posterior semicircular canal. Pink: saccular macular (situated within the sacculus). Orange: utricular macular (situated within the utriculus); redrawn from Lisney (2010). (**d**) Electroreception showing the morphology of the ampullary electroreceptors in a skate redrawn from Baker et al. (2013). Purple: receptor cells. Pale blue: support cells. Aqua: conductive jelly. Orange: epidermal plug. Black: afferent nerves. (**e**) Generalized vertebrate taste bud showing light and dark sensory cells redrawn from Northcutt (2004). Yellow: light cells. Orange: dark

cells. Purple: basal cells. Gray: basement membrane. Black: afferent nerves. (**f**) Lateral line system represented by a longitudinal section of the lateral canal in *Carcharhinus* redrawn from Tester and Kendall (1969). Purple: cupula. Green: neuromast zone. Yellow: fiber zone. Red: blood vessels. Black: nerves. Drawings by CB

Odors are detected by the **sensory epithelium** (Vogel 1994) located in sensory channels made from the secondary folds of opposing **lamellae**, in the olfactory lamellar arrays in the nasal sacs (Fig. 4.6b; Howard et al. 2013). The arrangement of the lamellae differs between holocephalans and elasmobranchs. In holocephalans, there are fewer lamellae (25–36) arranged in a radial fashion around an elliptical central port, whereas neoselachians have linear arrays that can accommodate up to 700 lamellae (Fig. 4.6b; Howard et al. 2013). The total area of olfactory lamellar area is sometimes used as a proxy for olfactory sensitivity (Kajiura et al. 2005; Holmes et al. 2011), and Theiss et al. (2009) suggest it is a better estimate of olfactory sensitivity than lamella number. Neoselachians, especially ambush predators like wobbegongs (Theiss et al. 2009), would have better olfactory sensitivity than holocephalans (Howard et al. 2013), but other features are also important in olfaction including the proportion of the lamellae surface actually covered in sensory receptors (Hara 1992), the geometrical array of the olfactory lamellae which allow for different numbers of lamellae (differ in different species, e.g., Meng and Yin 1981; Theisen et al. 1986), the width of the sensory channels (Levich 1962; Holmes et al. 2011), and the size of the olfactory bulb in the brain to process these stimuli (Yopak et al. 2015). The size of the olfactory bulb in chondrichthyans is tightly linked to their habitats rather than to phylogeny (Yopak et al. 2015). The largest olfactory bulbs occur in pelagic, coastal oceanic sharks such as the great white and tiger sharks, and this might be related to their reliance on olfaction for long distance migration and for the detection of food sources such as whale carcasses. Reef sharks of the same family (Carcharhinidae) as well as Hemiscylliidae and dasyatid batoids have the smallest olfactory bulbs of all species surveyed to date (Yopak et al. 2015). In the reef habitat, chondrichthyans rely on vision heavily. As for other senses, there is therefore a great variation of sensory abilities within the chondrichthyans.

Taste/Gustation

Taste buds are present in the mouth and neck (pharynx) of chondrichthyans, but their position and density vary between species (beige in Figs. 4.5 and 4.6; Northcutt 2004). In batoids, they are interspersed with **denticles**, which might protect against abrasion and parasites, reduce hydrodynamic drag from ram ventilation, and improve grasp and holding of prey (Rangel et al. 2016). The presence of denticles, however, reduces the surface area available for taste buds, which suggests that this generalist feeder does not have great taste capability, similar to other batoids (Atkinson and Collin 2012). In the spiny dogfish, the taste buds are most numerous on the roof of the mouth (Gardiner et al. 2012), while in the bamboo shark, they occur throughout the oral and pharyngeal region (Atkinson et al. 2016); a palatal organ was recently described for the rabbit fish (*Chimaera monstrosa*), common in all holocephalans (Ferrrando et al. 2016). This palatal organ has a low density of taste buds, so the primary use might be for general mechanical sensitivity involved in food sorting rather than tasting (Ferrrando et al. 2016).

The **taste buds** are pear-shaped multicellular chemoreceptors with apical (mouth) and basal (lying on the basement membrane) ends, oriented at a right angle to its position in the mouth (Fig. 4.6e; Northcutt 2004). The apical surface is the receptor area which has sensory cells consisting of large or small receptor villi (hair). At the apical surface are the light, main sensory cells (Fig. 4.6e,

yellow) and dark, secondary sensory cells (Fig. 4.6e, orange), which are responsible for collecting the taste input. They communicate to the basal cells (Fig. 4.6e, purple) that lie directly on the basement membrane and contain vesicles rich in serotonin communicating with the nerves to relay messages to the brain. Stem cells are also present in the basal membrane, presumably for regeneration of the taste buds (Martin et al. 2016). The taste buds are innervated by branches of facial, **glossopharyngeal,** and **vagal** nerves. Although taste receptors in chondrichthyans closely resemble those of other vertebrates (Gardiner et al. 2012), there is a lot of variation in the oral papillae morphology with more than one type occurring in one species (Rangel et al. 2016).

Vision

In most chondrichthyan species, vision plays a role in spatial orientation, navigation, communication, and predatory and social behavior (Figs. 4.5 and 4.6a, blue; Lisney et al. 2012). Eye size relative to body size is an indicator of the relative importance of vision and is linked to habitat type (shallow vs. deep water), activity level, and prey type (Gardiner et al. 2012). The sharks with the largest eyes are thresher sharks that make deep vertical migrations (DVM), diving down more than 600 m within 10 min, and deep-sea sharks. Bigger eyes might be needed to adapt rapidly to light differences during DVM and for increased light sensitivity in species living in deep-sea habitats but also breeding in shallow water environments like the holocephalan *Callorhinchus milii* (Lisney 2010). The smallest eye size is found in benthic (bottom dwelling) sharks and batoids from coastal habitats where the water is turbid (Lisney and Collin 2007) and in some deep-sea batoids such as *Benthobatis* sp. and *Typhlonarke* sp., where the eyes are degenerate (Gruber 1977; Locket 1977).

The position of the eyes in elasmobranch depends on their habitats. Pelagic and benthopelagic species have laterally positioned eyes whereas benthic (bottom dwelling) batoids have dorsolateral eyes (Gardiner et al. 2012). There is only scarce data about the **visual field** of elasmobranchs, which is defined as the area seen without moving the eyes. It ranges from c. 104° to 196° in the vertical plane and 159° to 199° in the horizontal plane (Lisney et al. 2012) but is monocular in most species. There are areas of binocular overlap, but it varies from c. 7° to 48° in the horizontal plane and from 0° to 50° in the vertical plane and occurs at the expense of posterior blind areas (Lisney et al. 2012). The greatest anterior binocular overlap is in the hammerhead sharks and is was linked with the lateral head expansion in these species. To overcome anterior blind spots, hammerheads move their heads side to side more than other species (greater yaw) when swimming (McComb et al. 2009). Hammerheads aside, batoids with dorsolaterally placed eyes have greater areas of binocular overlap in the horizontal plane compared to sharks which have lateral eyes. However, the dynamic visual field can be extended to 360° when swimming and moving the eyes (Gardiner et al. 2012).

Sharks have at least an upper and lower eyelid with some sharks, like lemon sharks, having the **nictitating membrane**, acting as a third eyelid to protect the eye from abrasion during feeding. Great white sharks and whale sharks rotate their eyeball while feeding to protect them from abrasion (Gardiner et al. 2012).

As in other vertebrates, light enters through the **cornea** (Fig. 4.6a, pale green) and **pupil** and is focused onto the **retina** (at the back of the eye, purple) by the **lens** (gray), which can be moved by the **intraocular muscles** such as the **pseudocampanule** (**protractor lentis**) (dark blue). The shape of the pupil varies according to habitat and behavior. It can be round as in deep-sea sharks, crescent-shaped in many skates and rays to camouflage the eye from predators and reduce the effects of spherical aberration (Lisney et al. 2012), or a slit in active predators like lemon sharks as it is the most mechanically efficient way to close down the pupil to a pinhole and allows the sharks to be active both during the day and night (Gardiner et al. 2012). The degree with which the

pupil can be closed depends on light levels and activity pattern. It is almost immobile in low-light habitats and can constrict rapidly in sharks active both during night and day (Lisney et al. 2012).

Color Vision in Sharks?

There are visual and non-visual pigments in the eyes of chondrichthyans. The non-visual pigments are present in the **cornea** (Fig. 4.6a, pale green), **aqueous** (pale orange) and **vitreous humors** (yellow), and the **lens** (gray) to filter out wavelengths such as damaging UV light and to remove light prone to scatter. It is present mostly in surface dwellers. Additionally, chondrichthyans have a structure composed of mirror-like crystals (the **tapetum lucidum**) in the **choroid** (brown) behind the **retina** (purple). The tapetum lucidum is responsible for the eye shine in many vertebrates and is an adaptation for low-light conditions. It acts by reflecting light back to the photoreceptors layer of the retina and gives photons a second opportunity to excite the photoreceptors, hence increasing visual sensitivity (Ollivier et al. 2004). It is found in all chondrichthyan species (Lisney et al. 2012) and has different spectral properties depending on the width and spacing of the guanine crystals it contains, reflecting bluer light in deep-sea species and green blue in coastal species.

Visual pigments are located in photoreceptor cells classified according to their morphology and light sensitivity. **Rods** are highly sensitive to light but have low visual acuity (used in low-light conditions), and **cones** are used for bright light and color vision and are responsible for higher visual acuity (Lisney et al. 2012). The great majority of chondrichthyans have retinas containing both cones and rods, and the proportion of cones to rods in some species is relatively high. Species living in low-light conditions like deep-sea rays and the Port Jackson shark (living in turbid shallow water) have all-rod retinas indicating that they are possibly color blind (Bozzano et al. 2001; Bozzano 2004; Lisney et al. 2012). The presence of both cones and rods is not the only indicator of color vision, as at least two types of cones are required for color differentiation (Gardiner et al. 2012). The cones become specialized with visual pigments sensitive to specific wavelengths and intensity of light. Each visual pigment is composed of an **opsin** protein and a **chromophore,** and it is the properties of the chromophore that define the spectral sensitivity of the pigment as a whole. In vertebrates, there is only one class of medium-wavelength-sensitive pigments on rod photoreceptors for low-light vision, whereas there are four classes of pigments on cones with sensitivities ranging from long wavelength (λmax c. 500–575 nm) to UV and violet wavelength (λmax 355–445 nm) (Hunt et al. 2009). Deepwater species have photoreceptors shifted toward shorter wavelengths (blue) as ocean water becomes blue and monochromatic at depth, and these photoreceptors are better at detecting bioluminescence, the only source of light below 1000 m (Lisney et al. 2012). Sharks (selachians) appear to only have one cone type (Hart et al. 2011), so it is likely that sharks do not have **color vision**. In contrast, there is evidence that at least one deep-sea holocephalan *Callorhinchus milii* (Davies et al. 2009, 2012) and a number of species of rays (Hart et al. 2004; Theiss et al. 2007) do have multiple cone types suggesting that they have color vision. To date, very few behavioral experiments exist to demonstrate color detection when brightness is controlled as a factor. It has been found that the giant shovelnose ray could discriminate colors (Van-Eyk et al. 2011), but Schluessel et al. (2014) found that the bamboo shark was color blind but could distinguish different intensities very well. More behavioral experiments would be needed, but as many sharks are hard to keep in captivity or difficult to observe in the wild, most of the known data about color vision in elasmobranch is derived from anatomical observations (Lisney et al. 2012).

Hearing and Mechanosenses

Chondrichthyans are not known for making any sound (Gardiner et al. 2012) but can detect both sound through the **inner ear** (Fig. 4.6c) and vibrations through the **lateral line system** (Fig. 4.6f). Both senses are part of the **acousticolateralis system** which plays an important role in prey,

predator, and conspecific detection as well as in orientation in relation to currents and hydrodynamic imaging (Lisney 2010). Chondrichthyan external ears consist of two small openings behind the eyes; they lack accessory organs like a swim bladder and a body connection between the swim bladder and the inner ear. They detect sound using the inner ear which is similar in structure to that of bony fishes (Lisney 2010). The inner ear consists of a **labyrinth** made up of several canals and sacs filled with a liquid (the **endolymph**). The three major canals are the anterior (ASC; Fig. 4.6c, yellow), posterior (PSC, green), and horizontal (HSC, blue) **semicircular canals** that are oriented in different planes and are responsible for detecting turning motion but are not involved in detecting sound. The three sac-like structures at the base of the labyrinth are the **lagena** (LM, Fig. 4.6c, purple), **sacculus** (SM, pink), and **utriculus** (UM, orange), which are involved in both balance and hearing (Lisney 2010). These structures contain **hair cells** called **maculae** which are associated with the eighth cranial (auditory) nerve (Fig. 4.5) and whose sensory hairs are covered by mineralized ear bones (**otoconia**) similar to bony fishes' otoliths (Lisney 2010). When sound enters the inner ear and hits the otoconia, the amplitude of the sound wave changes because of the different density of the otoconia relative to the water. This causes the hair cells to move, which is then transmitted as a nerve impulse to the auditory nerve. As well, chondrichthyans have an additional macula (area of neuromast-based sensory epithelium) called the **macula neglecta** (MN, Fig. 4.6c red). It is not covered by otoconial mass but is associated with the posterior semicircular canal (green) and is important for sound detection at least in elasmobranchs (Lowenstein and Roberts 1951; Fay et al. 1974; Corwin 1989). Free-swimming, piscivorous elasmobranchs tend to have a larger sacculus and posterior semicircular canal duct and a more complex, larger macula neglecta than bottom-dwelling, non-piscivorous species which suggests that the former have better hearing than the latter (Myrberg 2001). In chimaerids (the only holocephalans studied), there is a connection between the anterior and posterior semicircular canals which is lacking in elasmobranchs, and the saccular and utricular regions are not separated. This might represent specializations for sound detection, but the functional significance of these morphological differences is still unclear (Lisney 2010). Only a handful of elasmobranch species were tested for hearing, but their behavior and audiograms show that they can be attracted and detect low-frequency sounds (Myrberg 2001). In addition, lemon sharks can localize the source of a sound to around 10° (Nelson 1967), and blacktip sharks have been shown to be able to detect changes in barometric pressure as low as 5 mb to avoid storms. This is because the vestibular hair cells of their inner ear respond to changes in hydrostatic pressure (Heupel et al. 2003).

The second component of the acousticolateralis system is the **lateral line system** (Fig. 4.6f) which is a system of canals and superficial receptors around the snout and midline of all chondrichthyans involved in sensing water current, pressure waves, and, to a certain extent, sound (Gardiner et al. 2012). The functional units in the lateral line are the **neuromasts** (Fig. 4.6f, green), which are clusters of ciliated sensory cells as well as support cells encapsulated into a jelly-like sheath called the **cupula** (purple) which can be stimulated by water movement or pressure (Lisney 2010). They work in a similar way to the inner ear cells where water movement over the cupula and the sensory hairs transforms mechanical energy into a neuronal impulse transmitted to the **medulla** in the brain (Fig. 4.5a) (Maruska 2001). There are several types of mechanosensory lateral line organs: the superficial neuromasts (pit organs) which are located on the skin surface either in grooves or between modified scales to protect them from forward-swimming motion; canal neuromasts which are either connected to the outside environment by pores (pored) or isolated from it (non-pored) or located in a system of open grooves in chimaerids; spiracular organs which are stimulated by flexion of the cranial-hyomandibular joint and are situated in the diverticula of the first visceral pouch; and the **vesicles of Savi** which are present in some groups of rays and consist of neuromasts enclosed in subepidermal pouches (Maruska 2001). The distance range and sensitivity of the lateral line system are determined by the distribution and morphology of these mechanoreceptors. The large concentration of non-pored canals around the nose and mouth may function as specialized tactile receptors stimulated by prey contact and aid in feeding, and in

batoids, the vesicles of Savi around the mouth would help in prey localization. The pored canals on the dorsal surface of the body and tail of elasmobranch could be used to detect water movement from conspecifics, predators, and currents (Maruska 2001). Although there is great diversity in the morphology of lateral line canals in chondrichthyans, much remains to be understood about its functional significance.

AQ6

Electroreception (Ampullae of Lorenzini)

Chondrichthyans can detect small electric fields coming from other living organisms (biotic sources) as well as from physical sources such as geomagnetic induction of electric currents (abiotic sources) which aids in prey capture and orientation (Lisney 2010). Structures involved in this detection are called **ampullae of Lorenzini** in elasmobranch and **electroreceptive ampullae** in holocephalans and are homologous to each other (Fig. 4.6d). In marine elasmobranchs, ampullae are grouped together in bilateral head clusters that radiate in many directions and terminate in individual pores (Gardiner et al. 2012). This allows the electric potential of different **ampullae** within a cluster to be compared and the voltage difference between them to be measured. In holocephalans, the ampullae are also grouped in a number of distinct clusters but are associated with the lateral line canals (Lisney 2010). The **ampullary electroreceptors** (ampullae) consist of **sensory** (purple) and **support cells** (pale blue) located at the base of a canal filled with a low resistance **conductive jelly** (aqua). The tight junction of the canal wall and between the sensory and support cells serves as an electrical barrier. Current is detected as the difference between voltages at the top (apical) vs. base (basal) surface of the sensory cells. Ampullae are very sensitive, and elasmobranch can detect voltage gradients as low as 1–5 nV/cm (Tricas and Sisneros 2004). An animal's electroreceptive capabilities are likely to be determined by the density and distribution of the ampullary organ as well as the shape of the head (Lisney 2010). For example, the hammerhead sharks have an enlarged snout and have a larger number of ampullae and higher pore density than similarly sized carcharhinids, suggesting that they have better electroreceptive capability (Kajiura 2001). In most chondrichthyan species, electroreception is believed to be most important in prey detection and capture, but it has been shown to also be important in social communication such as mate and predator detection as well as the detection of magnetically induced fields involved in orientation behaviors (Lisney 2010). As for other senses, much is to be learned about the electrosensory abilities of chondrichthyans.

Conclusions

Chondrichthyans have evolved over 400 million years ago and have been incredibly morphologically diverse. They have survived large mass extinction events affecting vertebrates at the end of the Devonian and Permian geological periods, and although less diverse than at their peak in the Paleozoic, they are still ecologically and morphologically diverse today. Chondrichthyans are an excellent developmental model for understanding gnathostome evolution, possessing a suite of phylogenetically basal characters and long gestation periods in ovo to allow for developmental manipulation. The broad range of ecological adaptations has made chondrichthyans successful in the past, but many species are under increasing threat of extinction due to fishing, poor preservation status, habitat destruction, and human-induced climate change. Current conservation bodies are working hard to change the public perception, and it is hoped that we can make sure chondrichthyans thrive and continue to amaze us with their diversity and beauty.

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