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FREDERICK W. HARRISON

Olfactory Morphology of Carcharhinid and Sphyrnid Sharks: Does the Cephalofoil Confer a Sensory Advantage?

Stephen M. Kajiura,[1]* **Jesica B. Forni,**[2] **and Adam P. Summers**[2]

[1]*Department of Biological Sciences, Florida Atlantic University, Boca Raton, Florida 33431*
[2]*Ecology and Evolutionary Biology, University of California, Irvine, California 92697*

ABSTRACT Many hypotheses have been advanced to explain the adaptive significance of the sphyrnid cephalofoil, including potential advantages of spacing the olfactory organs at the distal tips of the broad surface. We employed comparative morphology to test whether the sphyrnid cephalofoil provides better stereo-olfaction, increases olfactory acuity, and samples a greater volume of the medium compared to the situation in carcharhiniform sharks. The broadly spaced nares provide sphyrnid species with a significantly greater separation between the olfactory rosettes, which could lead to an enhanced ability to resolve odor gradients. In addition, most sphyrnid species possess prenarial grooves that greatly increase the volume of water sampled by the nares and thus increase the probability of odorant encounter. However, despite a much greater head width, and a significantly greater number of olfactory lamellae, scalloped hammerhead sharks do not possess a greater amount of olfactory epithelial surface area than the carcharhiniform sandbar sharks. Therefore, sphyrnid sharks might not possess any greater olfactory acuity than carcharhinids. Despite this, there are clear olfactory advantages to the cephalofoil head morphology that could have led to its evolution, persistence, and diversification. J. Morphol. 264:253–263, 2005. © 2004 Wiley-Liss, Inc.

KEY WORDS: Carcharhinidae; Sphyrnidae; lamellae; nares; olfactory rosette; prenarial groove

"…it would appear that the fish, by a sort of centrifugal action, go on shaking out the comparatively soft materials of the head more and more to the sides." (Kyle, 1926)

The eight species of hammerhead sharks (Carcharhiniformes, Sphyrnidae) possess a head morphology that is unique among extant vertebrate taxa. Their name is derived from their dorsoventrally compressed and laterally expanded neurocranial morphology, which, when viewed dorsally, resembles a doubled-ended mallet or hammer. This peculiar cranial morphology has been termed the "cephalofoil" in recognition of its wing-like appearance (Compagno, 1984, 1988). Various hypotheses have been advanced to explain the function and adaptive significance of the cephalofoil but only a few have been empirically tested (Table 1). Several hypothetical sensory advantages have been ascribed to the cephalofoil including various perceived advances in olfactory capability. The olfactory hypotheses fall into three categories: 1) enhanced olfactory klinotaxis, 2) increased olfactory acuity, and 3) larger sampling swath of the surrounding medium.

To put these hypotheses into a quantifiable context, consider the probability that an odorant molecule binds to a receptor in the nasal rosette. The number of odorant molecules that cross the olfactory epithelium is:

$$\dot{N}(\text{moles sec}^{-1}) = C(\text{moles cm}^{-3}) A_n(\text{cm}^2)V(\text{cm sec}^{-1}) \quad (1)$$

where C is the concentration of odor molecules, A_n is the area sampled by the naris, and V is the velocity of odorant over the olfactory rosette (Fig. 1). The stimulus strength (S) is:

$$S \propto \dot{N}(\text{moles sec}^{-1})A_r(\text{cm}^2)t(\text{sec}) \quad (2)$$

where the number of receptors is assumed to be proportional to the area of the sensory epithelium (A_r), and t is the time a molecule spends in the rosette.

Olfactory klinotaxis is the ability to compare odorant stimulus intensities between left and right nasal rosettes and orient toward the side with the greatest intensity. The left and right rosettes sample the same area at the same velocity, so S will depend only on the concentration of odorant at each rosette. The greater the distance (d) between the rosettes, the larger the difference between S_{right} and S_{left}. The broadly separated incurrent nares located at the distal tips along the anterior margin of the cephalofoil allow the hammerhead sharks to sample more

TABLE 1. Hypotheses advanced for the adaptive function of the sphyrnid cephalofoil along with the earliest known record of each stated hypothesis and specific test of the hypothesis

Hypothesis	Proposed	Tested
Binocular vision	Compagno, 1984	Untested
Stereo-olfaction	Hasler, 1957	This study
Electroreception	Compagno, 1984	Kajiura and Holland, 2002
Lateral line	Compagno, 1984	Untested
Hydrodynamic lift	Aleev, 1969	Nakaya, 1995 (partial)
Maneuverability	Springer, 1967	Kajiura et al., 2003
Prey handling	Strong et al., 1990	Untested

distantly spaced regions of an odorant plume than the more closely spaced nares of a typically pointed snout, carcharhiniform shark. Assuming the sharks are able to perform olfactory klinotaxis, the larger difference between S_{right} and S_{left} will make it easier to localize the odor source (Hasler, 1957; Nelson, 1969; Johnsen and Teeter, 1985).

Alternatively, or additionally, the laterally expanded cephalofoil provides sphyrnid sharks with a larger nasal capsule which could accommodate a longer nasal rosette (Compagno, 1984, 1988). A larger nasal rosette would have a greater surface area (A_r), providing more space for more chemosensory cells than in a carcharhiniform shark. More chemosensory cells increase the probability of an odor molecule binding to a receptor and triggering a neural response, thus providing hammerhead sharks with a greater olfactory acuity.

One further consequence of the wide cephalofoil is the broad swath of water swept by the head. If the nares are similarly expanded, then the area sampled for odorant (A_n) is increased, thus increasing the probability of an odor molecule binding to a receptor. Furthermore, most hammerhead shark species have a prenarial groove that extends medially from the incurrent nares along the anterior margin of the cephalofoil (Gilbert, 1967; Compagno, 1988). These grooves channel water along their length into the nares (Tester, 1963). Thus, the prenarial grooves effectively increase the width of the incurrent nares. If the nares themselves are not broader in hammerheads than in carcharhiniform sharks, then perhaps these prenarial grooves serve to increase the sampled area.

These three distinct olfactory-related functions of the cephalofoil have been proposed as selective forces favoring the evolution of the hammerhead cephalofoil. However, there exists little or no empirical evidence to support the current utility of the cephalofoil as an olfactory enhancement. Before the issue of historical utility can be addressed, we need some basis for ascribing a sensory advantage in extant hammerhead sharks. The goals of this study were to 1) determine whether hammerhead sharks have greater separation between left and right nares, supporting the possibility of enhanced olfactory klinotaxis; 2) assess olfactory acuity by comparing the surface area and rosette morphology between hammerhead and carcharhiniform sharks; 3) examine changes in the olfactory rosette with growth in both a hammerhead shark and a carcharhiniform shark; and 4) measure the area sampled by sharks with disparate head morphologies.

MATERIALS AND METHODS
Collection and Preservation

Head morphology data were collected from representatives of all eight hammerhead shark species (*Eusphyra blochii, Sphyrna mokarran, S. lewini, S. zygaena, S. corona, S. media, S. tudes, S. tiburo*) and from two carcharhinid species (*Carcharhinus*
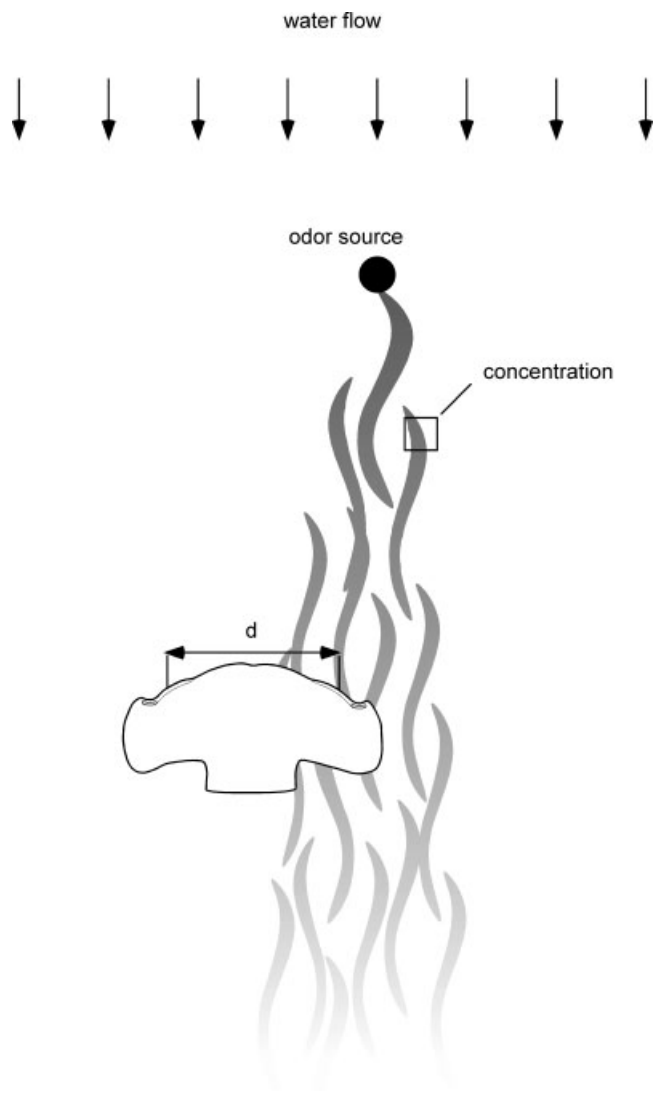

Fig. 1. Schematic diagram of a sphyrnid shark head in an odor plume. A greater chemical concentration is indicated by darker shading. The distance (d) between the midpoints of the effective sampling length indicates the ability to resolve odors to the left and right sides of the head. The difference in odor concentration across the width of the cephalofoil is greater for sharks with widely spaced nostrils.
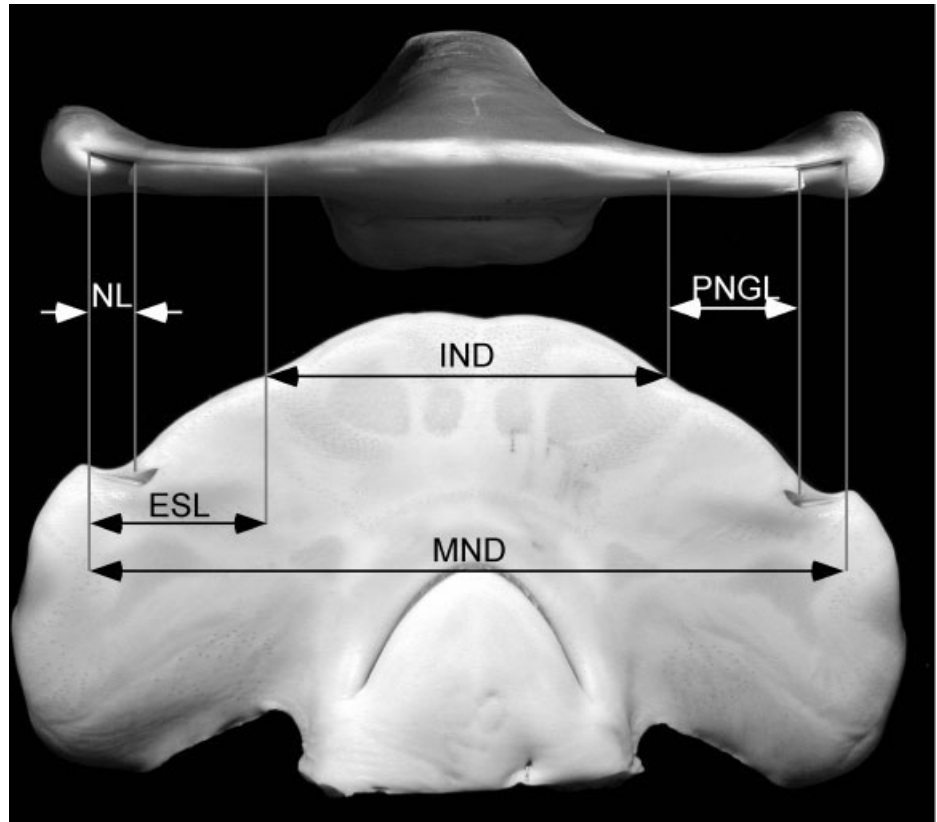
Fig. 2. Morphometric measurements illustrated on the head of a representative scalloped hammerhead shark, *Sphyrna lewini*. Narial length (NL) and prenarial groove length (PNGL) are combined to form the effective sampling length (ESL). The distance between the medial edges of the prenarial grooves forms the internarial distance (IND) and the distance between the lateral edges of the incurrent nares forms the maximum narial distance (MND).

plumbeus, Scoliodon laticaudus). Juvenile sandbar sharks (*C. plumbeus*) are pointed snout carcharhiniform sharks that live in similar habitats and feed on similar prey items as juvenile scalloped hammerhead sharks (*S. lewini*) (Clarke, 1971; Medved et al., 1985), and the spadenose shark (*S. laticaudus*) is the carcharhiniform shark that is most closely related to the hammerhead clade (Compagno, 1988; Naylor, 1992).

All sharks used in this study were either incidental mortalities from other research projects or were museum specimens. Large numbers of fresh specimens were available for three species, the scalloped hammerhead shark, *Sphyrna lewini*, the bonnethead shark, *S. tiburo*, and the sandbar shark, *Carcharhinus plumbeus*. Of the three species for which fresh specimens were available, the bonnethead sharks (*S. tiburo*) were collected by long-line fishing, rod and reel fishing, or by gill net sets throughout coastal Florida and the Florida Keys. The sandbar sharks (*C. plumbeus*) were collected by long-line fishing outside Kaneohe Bay, Oahu, Hawaii. Most of the scalloped hammerhead sharks (*S. lewini*) were collected by hand-line fishing within Kaneohe Bay, with a few larger individuals collected from the south shore of Oahu. Sharks collected by us were fixed in 10% formalin then soaked for 24–48 h in several changes of fresh water. The specimens were then transferred through a graded isopropyl alcohol series (10, 20, 40%), then stored in 40% isopropanol. Because most of the head measurements were closely tied to skeletal structures, shrinkage artifacts due to preservation were minimal. The remaining shark species were sampled from either the ichthyology collection at the Los Angeles County Museum of Natural History or the U.S. National Museum of Natural History (Appendix).

Head Morphology

Various morphological features of the head of all species were measured to the nearest millimeter and a digital caliper was used to measure narial length (NL) to the nearest 0.01 mm (Fig. 2).

The maximum narial separation distance (MND) was measured from the lateralmost extent of the incurrent nares. For the carcharhinid sharks, the internarial separation distance (IND) was measured from between the medial margin of the incurrent nares. Most sphyrnid shark species possess a prenarial groove that extends medially from the incurrent nares, along the anterior margin of the cephalofoil, and effectively increases the narial length. Therefore, for sphyrnids, the internarial separation distance was measured from between the medial extent of the prenarial grooves. For the sphyrnid species that do not possess a prenarial groove (*Sphyrna corona, S. tiburo*), the internarial separation was measured as it was for the carcharhinid sharks. The prenarial groove length (PNGL) was measured from the medial edge of the prenarial groove to where the prenarial groove meets the medial margin of the incurrent naris. The narial length and prenarial groove length were combined to form the effective sampling length (ESL) for the sphyrnid sharks. For the carcharhinid sharks, the effective sampling length was equivalent to the narial length. Head measurement data were log transformed, tested for normality and homoscedasticity, and analyzed with an ANCOVA with total length of the shark as the covariate.

Olfactory Rosette

To determine whether the sphyrnid sharks possess a greater surface area of olfactory epithelium, the olfactory rosette morphology was compared between the sphyrnid and carcharhinid species. A camera lucida technique was used to trace the outline of the olfactory rosette in situ in a partially dissected head from each of the eight hammerhead shark species and two carcharhinid species. One of the paired olfactory rosettes was excised from at least one individual of each species and the total number of olfactory lamellae in the rosette was counted.

The surface area of the olfactory lamellae was estimated by subsampling seven individual lamellae that were evenly spaced
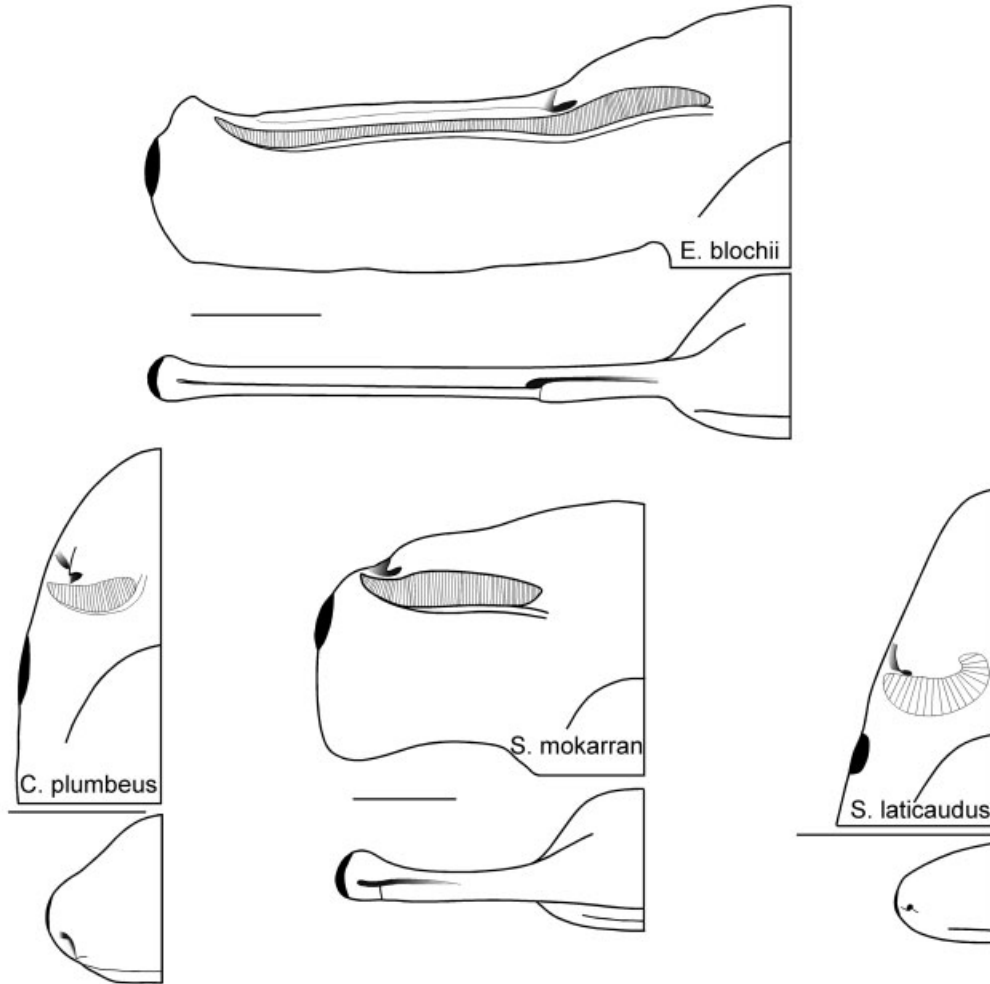
Fig. 3.   Frontal and ventral views of the head of all eight sphyrnid and two representative carcharhinid shark species. The position of the prenarial groove and incurrent naris are seen in the frontal view and the position of the olfactory rosette with respect to the incurrent and excurrent nares is seen in the ventral view. The relative number of lamellae comprising the rosette can be compared among species because each line represents two individual lamellae. Scale bar = 4 cm.

along the length of the rosette. These lamellae were placed individually on a microscope slide with a 5 mm calibration square and photographed with a digital camera. The surface area of each lamella was determined from the digital image (Image J). A Simpson's rule numerical integration was used to calculate the total lamellar surface area of the entire rosette from the surface area of the subsampled lamellae. Because the winghead shark, *Eusphyra blochii*, possessed approximately three times as many lamellae as the species with the next greatest number, 21 lamellae were sampled from the winghead shark. The calculated lamellar area was multiplied by four to account for surface area on both sides of the lamella and in both olfactory rosettes. The lamellar area data were log transformed and compared among species using an ANCOVA with total length of the shark as the covariate.

RESULTS

Head morphology and the morphology of the olfactory rosette differ dramatically among the eight hammerhead shark species (Fig. 3). Because the incurrent nares are associated with the anterolat-eral margin of the head, the diverse head morphologies result in differences in maximum narial separation distance. The maximum narial separation distance increased with shark total length for all species; however, only the winghead shark, *Eusphyra blochii*, the smooth hammerhead shark, *Sphyrna zygaena*, the scalloped hammerhead shark, *S. lewini*, and the sandbar shark, *Carcharhinus plumbeus*, could be tested statistically. There was a significant difference in maximum narial separation among all four species (ANCOVA, $F_{3,48} = 697.794$, $P < 0.0001$). *Eusphyra blochii* had the greatest maximum narial separation distance followed by *S. zygaena, S. lewini,* and *C. plumbeus* (Scheffé, $P < 0.0001$ for all four species).

Internarial separation distance increased with shark total length for all species and a significant difference was found between the winghead shark, *Eusphyra blochii*, the scalloped hammerhead shark,
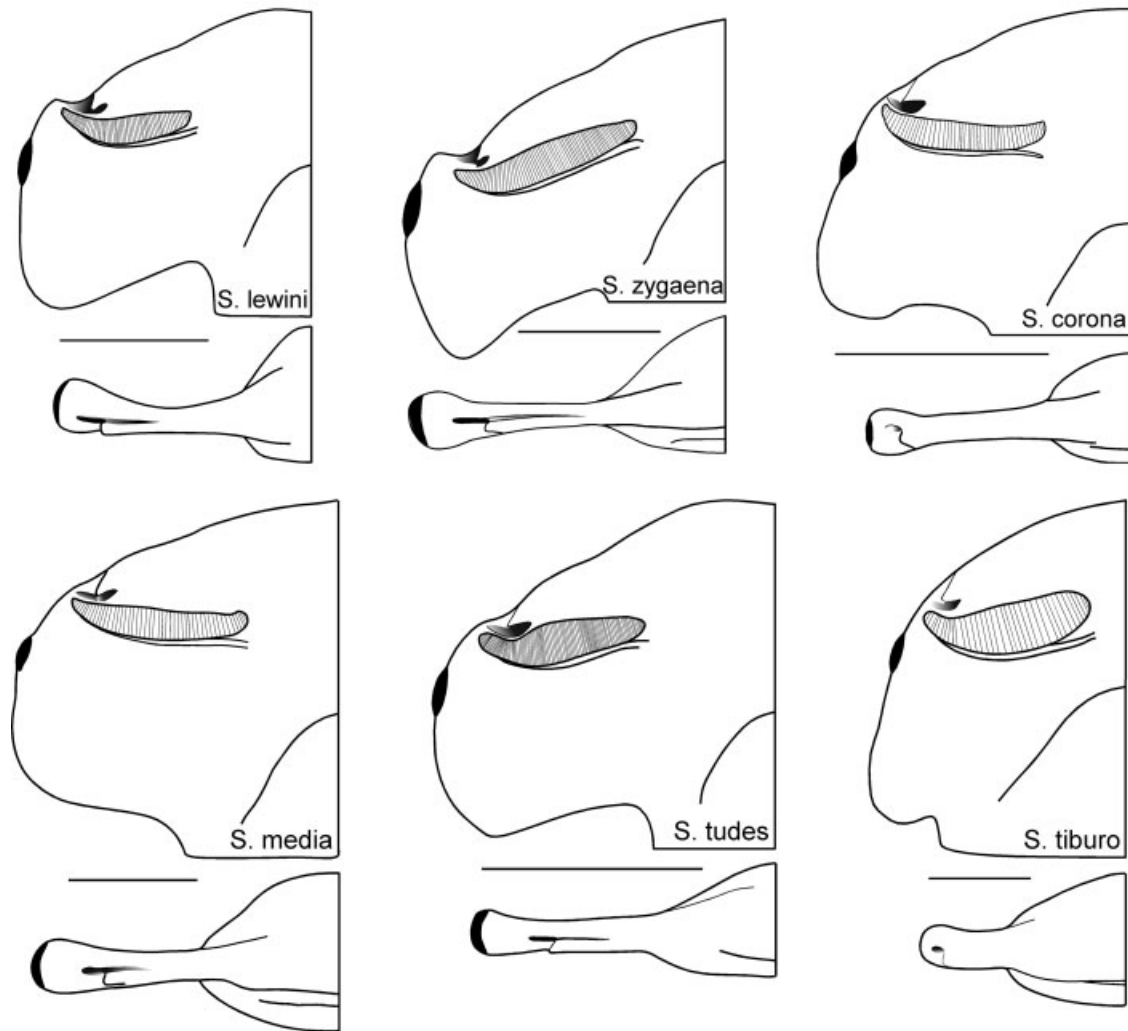
Figure 3. (Continued)

Sphyrna lewini, and the sandbar shark, *Carcharhinus plumbeus* (ANCOVA, $F_{2,40} = 111.851$, $P < 0.0001$). A Scheffé post-hoc test revealed that *S. lewini* had a significantly greater internarial separation distance than both *C. plumbeus* (Scheffé, $P < 0.0001$) and *E. blochii* (Scheffé, $P = 0.0015$); however, there was no significant difference between the latter two species (Scheffé, $P = 0.1174$).

The variable of greatest interest is neither the maximum narial separation nor the internarial separation distance but the separation distance between the midpoints of the left and right effective sampling lengths (Fig. 4). The mid-narial separation distance differed significantly between the winghead shark, *Eusphyra blochii*, the scalloped hammerhead shark, *Sphyrna lewini*, and the sandbar shark, *Carcharhinus plumbeus* (ANCOVA, $F_{2,42} = 483.420$, $P < 0.0001$). *Eusphyra blochii* had a significantly greater mid-narial separation distance than *S. lewini*, which, in turn, had a significantly greater

separation distance than *C. plumbeus* (Scheffé, $P < 0.0001$ for all three species).

Water enters the nasal capsule via the incurrent nares and a greater narial length will allow more water to enter. Because the other species demonstrated heteroscedasticity or significant interaction effects, the narial length was compared only between the scalloped hammerhead shark, *Sphyrna lewini* and the sandbar shark, *Carcharhinus plumbeus*. *Sphyrna lewini* possessed a significantly greater narial length than *C. plumbeus* (ANCOVA, $F_{2,76} = 554.769$, $P < 0.0001$). The winghead shark, *Eusphyra blochii*, is characterized by incurrent nares that are cumulatively open along almost two-thirds of the length of the cephalofoil, which allows the olfactory rosettes on either side to be directly exposed to the seawater (Fig. 3). Therefore, although the narial length of *E. blochii* was heteroscedastic and could not be tested statistically, it was obviously much greater than in any of the other species.
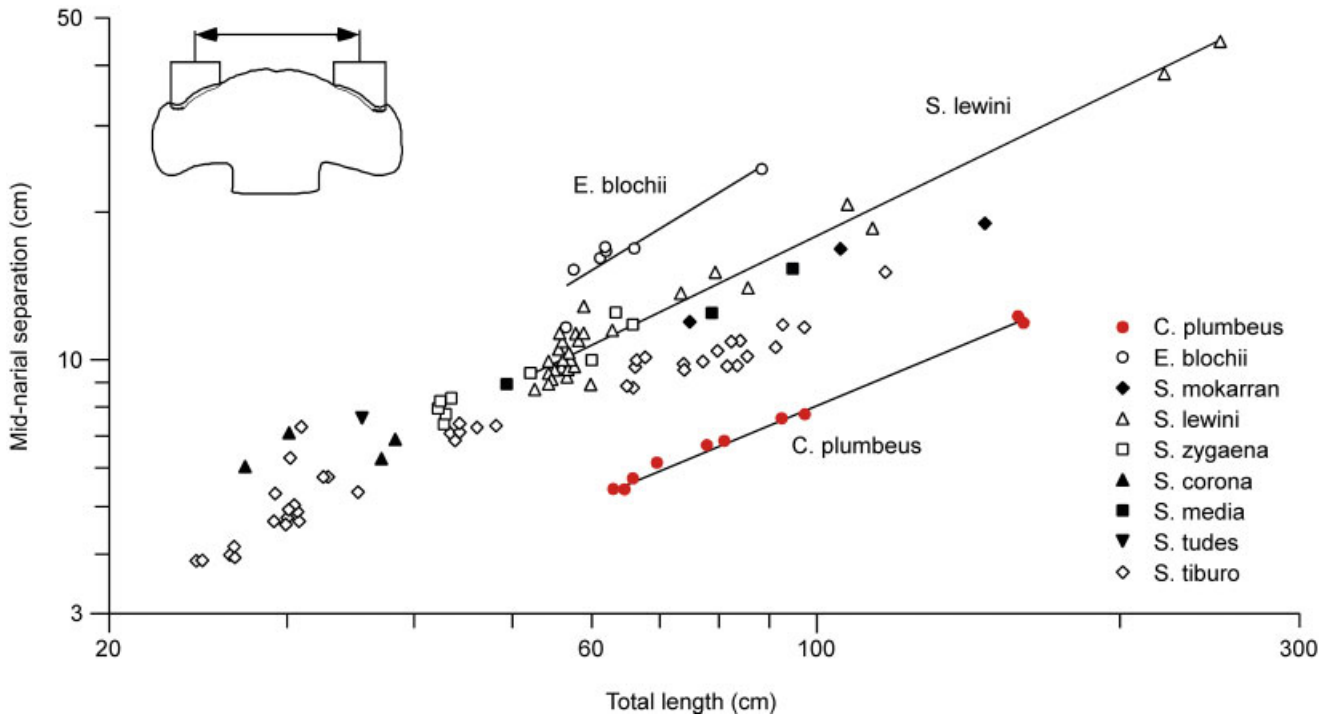
Fig. 4. The distance between the midpoints of the effective sampling length on left and right sides of the head plotted against total length of the shark. The mid-narial separation distance represents the functional separation distance between olfactory rosettes. Regression lines are shown for the species that were able to be tested statistically; *Eusphyra blochii* y = $0.0871x^{1.2607}$ R^2 = 0.8010, *Sphyrna lewini* y = $0.1759x^{1.0028}$ R^2 = 0.9642, *Carcharhinus plumbeus* y = $0.1525x^{0.8599}$ R^2 = 0.9925.

Water is sampled for odorant molecules from the medial end of the prenarial groove to the lateral edge of the incurrent naris. This effective sampling length (prenarial groove length + narial length) varied among the taxa and increased with shark total length (Fig. 5). The scalloped hammerhead, *Sphyrna lewini*, had a significantly greater effective sampling length than the sandbar shark, *Carcharhinus plumbeus* (ANCOVA, $F_{1,34}$ = 1974.235, $P < 0.0001$). The prenarial grooves combined with the extremely long incurrent nares of the winghead shark provide it with the greatest effective sampling length of any of the species, although heteroscedasticity prevented it from being compared statistically.

The scalloped hammerhead shark, *Sphyrna lewini*, had a greater number of olfactory lamellae than the bonnethead shark, *S. tiburo*, which in turn had a greater number than the sandbar shark, *Carcharhinus plumbeus* (ANOVA, $F_{2,38}$ = 1751.136, $P < 0.0001$; Scheffé, $P < 0.0001$ for all three species). Each of the remaining species was represented by only one or two individuals and was excluded from the statistical analysis, but the data are summarized in Table 2. Within each of the three species for which adequate sample sizes were available, there was no difference in total number of lamellae with increasing size (age) (*Sphyrna lewini* Regression, t = 1.285, P = 0.2252; *S. tiburo* Regression, t = -0.539, P = 0.5968; *Carcharhinus plumbeus* Regression, t = 1.285, P = 0.2252) or between the sexes (*S.*

lewini ANOVA, $F_{1,12}$ = 1.8975, P = 0.1957; *S. tiburo* ANOVA, $F_{1,19}$ = 0.1525, P = 0.7008; *C. plumbeus* ANOVA, $F_{1,7}$ = 0.4363, P = 0.5334).

Total lamellar surface area was determined for at least one individual from each species (Fig. 6) and for seven bonnethead shark individuals, *Sphyrna tiburo*, and six individuals from each of the scalloped hammerhead, *S. lewini*, and the sandbar shark, *Carcharhinus plumbeus*. There was a significant difference in lamellar area between the three species (ANCOVA, $F_{2,15}$ = 22.752, $P < 0.0001$). A Scheffé post-hoc test revealed that *S. tiburo* had significantly less lamellar area than either *S. lewini* (Scheffé, P = 0.0054) or *C. plumbeus* (Scheffé, P = 0.0084). However, there was no difference in lamellar area between *S. lewini* and *C. plumbeus* (Scheffé, P = 0.9768).

DISCUSSION

Our data suggest that there is a current utility to the cephalofoil in increasing olfactory abilities. The "enhanced olfaction" hypothesis can be decomposed into several component hypotheses, including enhanced stereo-olfaction, wider swath of water sampled by the nares, and greater olfactory acuity due to increased lamellar surface area. We addressed each of these components by comparing the peripheral olfactory system morphology of pointed snout car-
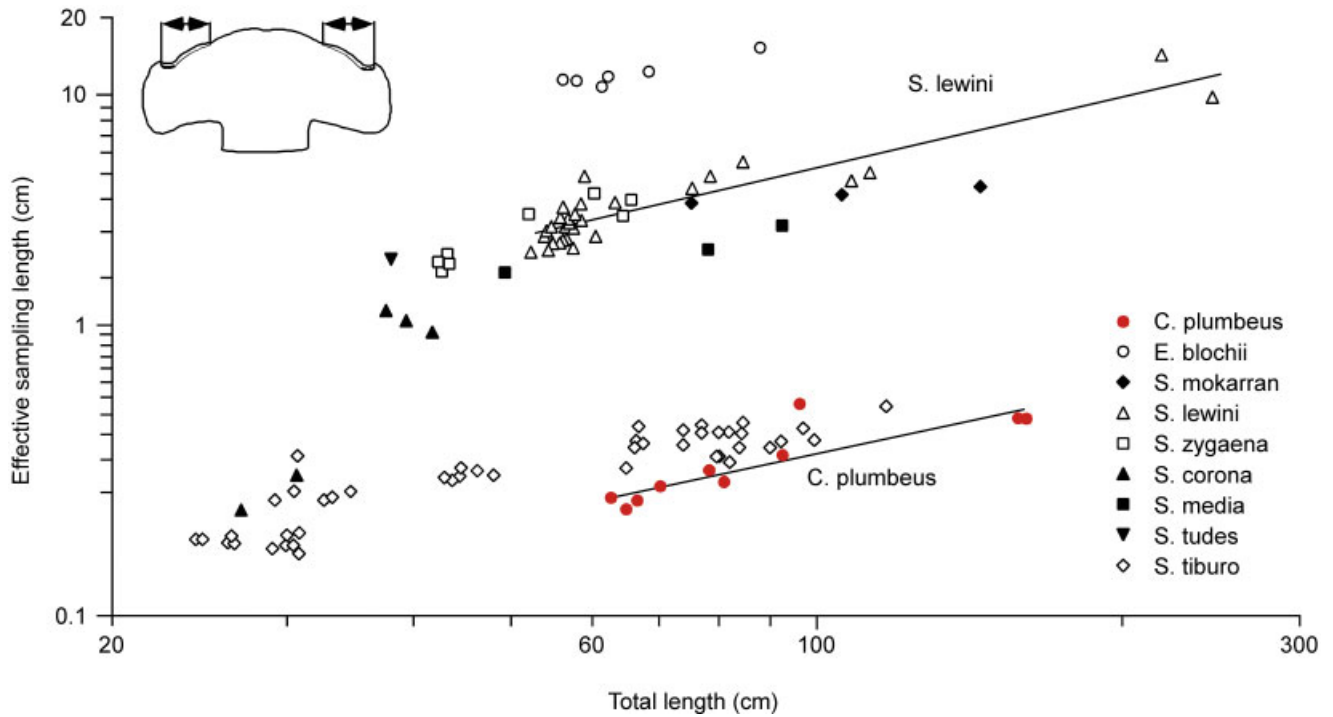
Fig. 5. The effective sampling length (narial length + prenarial groove length) plotted against total length for seven sphyrnid and one carcharhinid shark species. *Sphyrna tiburo, S. corona,* and *Carcharhinus plumbeus* are the only species that do not possess a prenarial groove and all have an apparently smaller effective sampling length than the other species. Regression lines are shown for the species that were able to tested statistically; *Sphyrna lewini* y = 0.0796x$^{0.9028}$ R^2 = 0.8576, *Carcharhinus plumbeus* y = 0.1525x$^{0.8599}$ R^2 = 0.9925.

charhinid sharks with that of sphyrnid sharks that possess a variety of head shapes.

It has been suggested that the widely spaced nares may allow the sphyrnid sharks to differentially sample odor gradients across the width of the cephalofoil, which could lead to true klinotaxis (Hasler, 1957; Nelson, 1969; Johnsen and Teeter, 1985). The morphology of the hammerhead shark seems well suited to klinotaxis because the maximum narial separation distance is larger in the hammerheads than in the carcharhiniform sharks. For example, a 60-cm total length winghead shark (*Eusphyra blochii*) has a maximum narial separation that is 6.5

TABLE 2. *Mean number of lamellae comprising the olfactory rosette for two carcharhinid and eight sphyrnid shark species*

Species	n	Mean ± SD # of lamellae
Carcharhinus plumbeus	11	57.7 ± 1.68
Scoliodon laticaudus	1	40
Eusphyra blochii	1	359
Sphyrna mokarran	2	134.0 + 2.833
S. lewini	13	124.2 + 2.54
S. zygaena	1	152
S. corona	1	96
S. media	1	98
S. tudes	1	97
S. tiburo	20	72.3 + 2.53

times that of a sandbar shark (*Carcharhinus plumbeus*) of the same size. However, maximum narial separation is only one determinant of stereo-olfaction. For a shark to be able to resolve odors across the width of the cephalofoil, the minimal separation between olfactory rosettes is also important. When this internarial distance is compared among the species, the scalloped hammerhead has ~73% greater separation than does the sandbar shark. We suppose that in an odor gradient, the more widely spaced incurrent nares of *Sphyrna lewini* will allow it to sample a greater difference in odor concentration, enabling klinotaxis in a more dilute odor plume.

It is interesting to note that although *Eusphyra blochii* and *Carcharhinus plumbeus* demonstrate the greatest difference in head width and maximum narial separation (Fig. 3), they do not differ significantly in internarial separation. The extremely wide head of *E. blochii* is characterized by not only wide nares, but also prenarial grooves that extend medially from the nares. These grooves greatly decrease the effective separation distance of the nares.

Another measure may provide a better metric of klinotactic ability. The effective sampling length (Fig. 2) assumes that odor molecules are sampled from along the length of the prenarial grooves and the incurrent nares. That being the case, olfactory
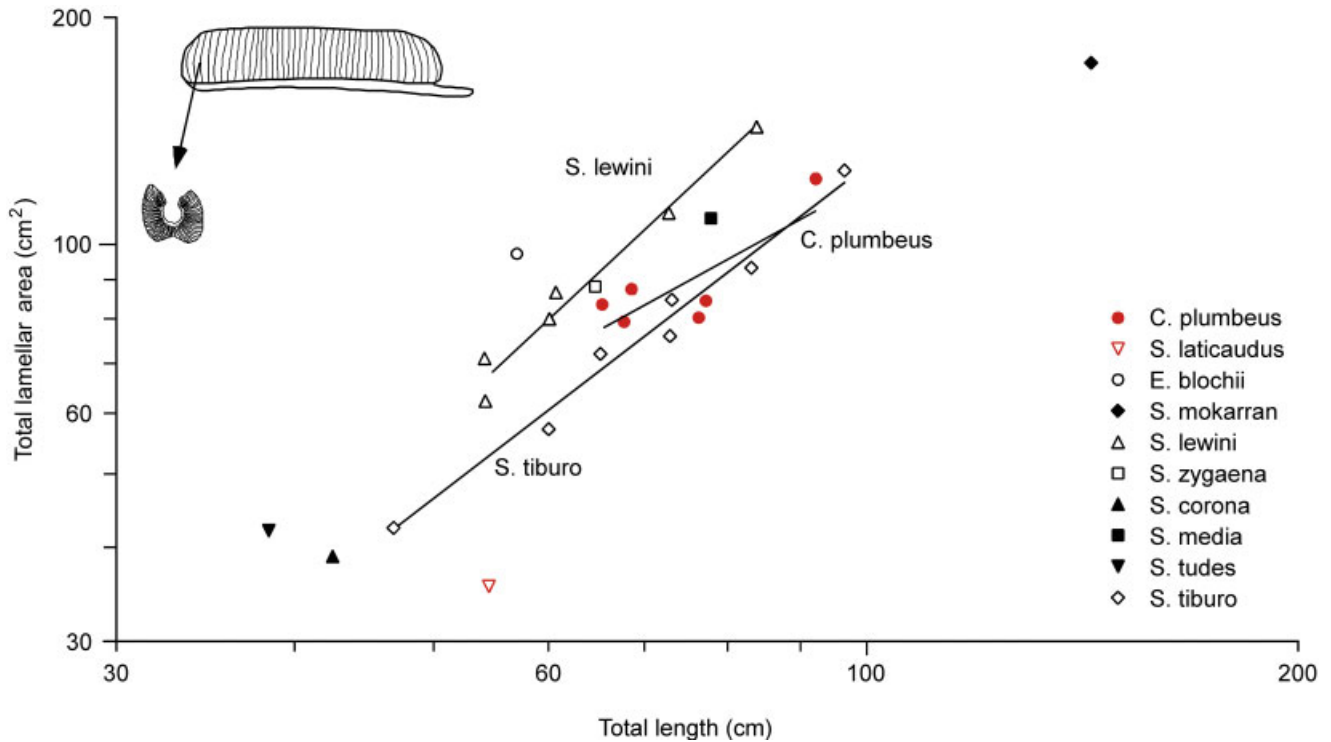
Fig. 6. Total lamellar surface area plotted against total length for eight sphyrnid and two carcharhinid shark species. Regression lines are indicated for only *Sphyrna lewini* $y = 0.056x^{1.7715}$ $R^2 = 0.9750$, *S. tiburo* $y = 0.1602x^{1.4477}$ $R^2 = 0.9837$ and *Carcharhinus plumbeus* $y = 0.9709x^{1.0463}$ $R^2 = 0.6631$; other species are represented by only single specimens. The total lamellar area does not differ significantly between the three species.

stimuli are integrated from along the entire effective sampling length. Therefore, the midpoint of the effective sampling length will determine the average olfactory intensity perceived by each naris. The difference in average signal strength is likely a determinant of klinotactic ability. The winghead shark, *Eusphyra blochii*, has 49% greater separation between the midpoints than the scalloped hammerhead shark, *Sphyrna lewini*, which, in turn, has 79% greater separation than the sandbar shark, *Carcharhinus plumbeus*. This indicates that the ability to resolve odors to left and right sides increases with increasing head width.

This study addressed only the morphological aspect of stereo-olfaction. It is important to put these data into a physiological context by employing behavioral assays to determine if sphyrnids and carcharhinids are equally capable of localizing a point odor source. It is clear that some sharks can localize odors (Table 3); however, direct comparative tests of localization efficiency between sphyrnid sharks and other species are lacking. True klinotaxis has been demonstrated for the bonnethead shark, *Sphyrna tiburo* (Johnsen and Teeter, 1985), but the protocol used would have likely elicited the same response from any shark species regardless of head morphology. Other species demonstrate nonklinotactic methods for orienting to an odor stimulus. Lemon sharks, *Negaprion brevirostris*, use rheotaxis—

turning into the current flow upon encountering an odor (Hodgson and Mathewson, 1971). Under most circumstances this will bring them to the source of the odor, although lemon sharks have also continued to swim upcurrent, past the odor source, presumably using only rheotactic orientation (Hodgson and Mathewson, 1978). In contrast, nurse sharks, *Ginglymostoma cirratum*, use true gradient searching (Hodgson and Mathewson, 1971) and are capable of localizing the general area of an odor source even in stagnant water (Kleerekoper et al., 1975).

Our data also support the second component of the enhanced olfaction hypothesis—that the wide

TABLE 3. Behavioral tests of the ability of sharks to directionally orient to an odor source

Order	Species	Reference
Orectolobiformes	*Ginglymostoma cirratum*	Hodgson and Mathewson, 1971
		Kleerekoper et al., 1975
Carcharhiniformes	*Mustelus canis*	Sheldon, 1911; Parker, 1914
	Negaprion brevirostris	Hodgson and Mathewson, 1971
	Sphyrna tiburo	Johnsen and Teeter, 1985

cephalofoil enables sphyrnid sharks to sample a wider swath of the seawater and thus have a higher probability of encountering odor molecules. The probability of an odor molecule impinging on the olfactory epithelium is a function of the width of the nares and the length of the prenarial groove. The prenarial grooves extend along the anterior margin of the cephalofoil and channel water into the incurrent nares on left and right sides of the head. This effectively extends medially the swath of water sampled by the nares creating an "effective sampling length" that is much greater than the narial length (Fig. 2). Scalloped hammerhead sharks, *Sphyrna lewini*, have an ~1,300% greater effective sampling length than similar-sized sandbar sharks, *Carcharhinus plumbeus*. This is due in part to the significantly greater narial length of *S. lewini* but mostly due to the presence of the long prenarial grooves. To put this in perspective, if both sharks cruised at 1.5 body lengths s^{-1}, a 1-m scalloped hammerhead would sample 810 cm^2 s^{-1} of water, whereas the same-size sandbar shark would sample only 62 cm^2 s^{-1}. Although the winghead shark, *Eusphyra blochii*, could not be tested statistically, it has by far the greatest effective sampling length due to its prenarial grooves coupled with its extremely long incurrent nares. As in the previous comparison, a 1-m winghead would sample 2,359 cm^2 s^{-1} of water. An additional peculiarity of the winghead incurrent nares is that they are open along much of the width of the cephalofoil, which allows the olfactory rosette to directly process seawater that contacts the anterior margin of the head.

Critical to the conclusion that the broad cephalofoil increases probability of odor encounter is the assumption that odorants are channeled along the prenarial grooves into the incurrent nares. Although this assumption has been supported (Tester, 1963), the experimental methods were not provided. The sinusoidal lateral undulations of the head as the shark swims could also influence how odors are channeled along the prenarial grooves. Requisite to understanding the processing of odorants is a determination of the temporal component of odorant sampling from the time an odorant reaches the prenarial groove until it elicits a neural response from the chemosensory cells within the lamellae. A detailed model of fluid flow around the cephalofoil is needed to address these questions.

Our data do not support the final component of the "enhanced olfaction" hypothesis for the evolution of the sphyrnid head morphology: an increased acuity with an increasing head width. It is proposed that the laterally expanded cephalofoil provides a larger nasal capsule volume that can accommodate a larger nasal organ with a greater number of chemoreceptor cells than a similar-sized carcharhinid shark. This does not appear to be the case. Although the scalloped hammerhead shark, *Sphyrna lewini*, had a significantly greater number of olfactory lamellae, it did not differ in lamellar surface area compared to the sandbar shark, *Carcharhinus plumbeus*. Interestingly, the bonnethead shark, *S. tiburo*, which has an intermediate head width morphology between *S. lewini* and *C. plumbeus*, had 11.6% less lamellar area than the sandbar and 15.0% less than the scalloped hammerhead.

That a hammerhead has less olfactory epithelium may seem paradoxical, but it is easily explained. Compared to carcharhinid sharks, the sphyrnids are characterized by a dorsoventrally compressed head morphology. This means that the size of individual lamellae is constrained by the olfactory capsule and cannot be as large as in carcharhinid sharks. The scalloped hammerhead shark possesses many more of these small lamellae, so that the total surface area is the same as the sandbar shark. The cephalofoil of the bonnethead is also dorsoventrally compressed, but is not nearly as broad as the scalloped hammerhead. Therefore, the lamellae of *Sphyrna tiburo* are small, as in *S. lewini*, but fewer lamellae are able to fit within the shorter nasal capsule, with the result that *S. tiburo* has a smaller total lamellar surface area than the other two species.

We recognize that total lamellar surface area is an incomplete indicator of potential sensitivity to odorants. Lamellae are characterized by secondary folds that greatly increase the surface area in contact with the seawater (Tester, 1963; Theisen et al., 1986; Zeiske et al., 1986, 1987). Although *Sphyrna lewini* and *Carcharhinus plumbeus* did not differ in total lamellar surface area, this was assessed only on a gross morphological scale. Our future research will examine the fine structure of the lamellae to determine if some species have a greater surface area due to more extensive folding of secondary lamellae. In addition, the density of the chemoreceptor cells within the lamellae must be assessed. Some species may possess a greater density of chemosensory cells, which would increase the signal-to-noise ratio and provide greater sensitivity. This is directly analogous to the number of sensory hair cells in the ampullae of Lorenzini, with more cells providing a greater signal-to-noise ratio of bioelectric fields (Raschi, 1986).

If chemosensory cell number is proportional to brain mass dedicated to olfactory stimulus processing, there is some indication that sphyrnids may have a greater chemosensory cell density than carcharhiniform sharks. The mass of the olfactory bulb of *Sphyrna lewini* is 7% of the total brain mass compared to an olfactory bulb mass of only 3% for *Carcharhinus plumbeus* (Northcutt, 1977). However, because the olfactory bulb extends along the length of the rosette and because the olfactory rosette of sphyrnid sharks is necessarily longer than that of carcharhinids (Fig. 3), the greater olfactory bulb mass may simply be a function of the size of the rosette, rather than a reflection of the number of receptor cells.

There are sufficient data for the scalloped hammerhead, *Sphyrna lewini*, the winghead, *Eusphyra blochii*, and the sandbar shark, *Carcharhinus plumbeus*, to make some observations about the scaling of the nares and olfactory epithelium with size. Narial widths are expected to scale with the length of the fish, as does any length (Schmidt-Neilsen, 1984). In *S. lewini*, the mid-narial separation, our favored metric of stereo-olfactory ability, scales with length, but in *E. blochii* it scales with an exponent of 1.2 and in *C. plumbeus* with an exponent of 0.85. As *E. blochii* individuals become larger, their klinotactic ability may increase disproportionately. Similarly, *C. plumbeus* individuals become relatively poorer at resolving an odorant field. The situation with the olfactory epithelium is different. The lamellar area should scale with the second power of length, and yet in all species it has a lower exponent (1.0–1.8). The sandbar shark is not adding nearly as much olfactory epithelial area as do the hammerheads as it grows, but even the hammerheads are below the line of isometry. This may be compensated for by an increased receptor density, or it may simply mean that as sharks get larger their chemosensory abilities become relatively less acute.

The olfactory system is in many ways analogous with the electroreceptive system of carcharhinid and sphyrnid sharks. Scalloped hammerhead sharks possess a significantly greater number of electrosensory pores than do sandbar sharks (Kajiura, 2001), but the absolute sensitivity to dipole electric fields does not differ between the species (Kajiura and Holland, 2002). Nonetheless, the wider cephalofoil allows the hammerhead sharks to sample a broader swath of the substratum in search of prey. For both electrosensory and olfactory systems, the wide cephalofoil increases the probability of detecting prey-generated stimuli, which would lead to a higher predation rate. Thus, both sensory systems are enhanced by being broadly spaced over the cephalofoil of sphyrnid sharks.

We have begun the process of testing the hypothetical selective forces that have shaped the head of the sphyrnid sharks. There remain several hypothetical uses for the head that are untested (i.e., lateral line, vision, and lift), and these should be the focus of future research. The development of a comprehensive phylogeny of the hammerhead sharks, in particular one that found their position within the paraphyletic carcharhinids, is of first importance because it will allow us to determine the evolutionary sequence of the morphological and physiological characters that we are measuring.

ACKNOWLEDGMENTS

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APPENDIX. Museum specimens from which olfactory rosettes were extracted for lamellae counts

Species	Sex	Total length (cm)	Museum	Specimen #
Scoliodon laticaudus	f	55.0	LACM	38130.059
Eusphyra blochii	f	61.5	LACM	38125.001
Sphyrna lewini	f	67.0	LACM	6853.040
Sphyrna zygaena	f	65.1	LACM	9335.003
Sphyrna corona	f	42.0	LACM	26162
Sphyrna media	m	77.5	LACM	6853.039
Sphyrna tudes	m	38.2	USNM	195957

LACM = Los Angeles County Natural History Museum, USNM = United States National Museum of Natural History.