

The pit organs of elasmobranchs: a review

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 The pit organs of elasmobranchs: a review

Meredith B. Peach1* **and N. Justin Marshall**²

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ch and Hearing Research Centre University of Queensland Brishane Queensland 4072** ²*Vision,Touch and Hearing Research Centre, University of Queensland, Brisbane, Queensland 4072, Australia*

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Elasmobranchs have hundreds of tiny sensory organs, called pit organs, scattered over the skin surface.
The pit Elasmobranchs have hundreds of tiny sensory organs, called pit organs, scattered over the skin surface.
The pit organs were noted in many early studies of the lateral line, but their exact nature has long
remained a myster Elasmobranchs have hundreds of tiny sensory organs, called pit organs, scattered over the skin surface.
The pit organs were noted in many early studies of the lateral line, but their exact nature has long
remained a myster The pit organs were noted in many early studies of the lateral line, but their exact nature has long
remained a mystery. Although pit organs were known to be innervated by the lateral line nerves, and
light micrographs sug remained a mystery. Although pit organs were known to be innervated by the lateral line nerves, and
light micrographs suggested that they were free neuromasts, speculation that they may be external taste
buds or chemorecep light micrographs suggested that they were free neuromasts, speculation that they may be external taste
buds or chemoreceptors has persisted until recently. Electron micrographs have now revealed that the pit
organs are in investigated. organs are indeed free neuromasts. Their functional and behavioural role(s), however, are yet to be investigated.
Keywords: pit organ; neuromast; lateral line; mechanoreceptor; shark

1. INTRODUCTION

The remarkable sensory abilities of elasmobranchs (sharks **EXECTS 1999 12:**
The remarkable sensory abilities of elasmobranchs (sharks
and rays) have inspired a great deal of research, literature
and popular entertainment. As top predators, their The remarkable sensory abilities of elasmobranchs (sharks
and rays) have inspired a great deal of research, literature
and popular entertainment. As top predators, their
sensory biology is of interest to fishers and ecolog and rays) have inspired a great deal of research, literature
and popular entertainment. As top predators, their
sensory biology is of interest to fishers and ecologists as
well as physiologists. One sensory system of elasm and popular entertainment. As top predators, their
sensory biology is of interest to fishers and ecologists as
well as physiologists. One sensory system of elasmosensory biology is of interest to fishers and ecologists as
well as physiologists. One sensory system of elasmo-
branchs, however, remains little known. The pit organs
are tiny sensory organs (in the order of 100 um diamet well as physiologists. One sensory system of elasmo-
branchs, however, remains little known. The pit organs
are tiny sensory organs (in the order of 100 µm diameter)
found scattered on the skin, mainly along the dorsal branchs, however, remains little known. The pit organs
are tiny sensory organs (in the order of 100 µm diameter)
found scattered on the skin, mainly along the dorsal
surface in species-specific patterns (Johnson 1917: Budk are tiny sensory organs (in the order of $100 \mu m$ diameter) found scattered on the skin, mainly along the dorsal surface, in species-specific patterns (Johnson 1917; Budker found scattered on the skin, mainly along the dorsal
surface, in species-specific patterns (Johnson 1917; Budker
1938; Tester & Nelson 1967; Maruska & Tricas 1998).
They are classified as part of the lateral line a sensory surface, in species-specific patterns (Johnson 1917; Budker
1938; Tester & Nelson 1967; Maruska & Tricas 1998).
They are classified as part of the lateral line, a sensory
system of fishes and larval amphibians (Blaxter 198 1938; Tester & Nelson 1967; Maruska & Tricas 1998).
They are classified as part of the lateral line, a sensory
system of fishes and larval amphibians (Blaxter 1987).
Details of the morphology of pit organs, however, are They are classified as part of the lateral line, a sensory
system of fishes and larval amphibians (Blaxter 1987).
Details of the morphology of pit organs, however, are
scarce, and their functional and behavioural role(s) system of fishes and larval amphibians (Blaxter 1987).
Details of the morphology of pit organs, however, are
scarce, and their functional and behavioural role(s) are
still obscure Details of the
scarce, and th
still obscure.
The latera scarce, and their functional and behavioural role(s) are still obscure.
The lateral-line system is mainly responsible for

still obscure.
The lateral-line system is mainly responsible for
detecting water motions of various kinds (see Blaxter's
(1987) review, and citations therein). The lateral-line The lateral-line system is mainly responsible for
detecting water motions of various kinds (see Blaxter's
(1987) review, and citations therein). The lateral-line
organs called neuromasts are mechanorecentors found detecting water motions of various kinds (see Blaxter's (1987) review, and citations therein). The lateral-line organs, called neuromasts, are mechanoreceptors found either on the skin surface or enclosed in subsurface can (1987) review, and citations therein). The lateral-line organs, called neuromasts, are mechanoreceptors found
either on the skin surface or enclosed in subsurface canals. organs, called neuromasts, are mechanoreceptors found
either on the skin surface or enclosed in subsurface canals.
Neuromasts typically contain sensory hair cells,
supporting cells and mantle cells, sitting on a basement either on the skin surface or enclosed in subsurface canals.
Neuromasts typically contain sensory hair cells,
supporting cells and mantle cells, sitting on a basement
membrane and canned by a gelatinous cupula into which Neuromasts typically contain sensory hair cells,
supporting cells and mantle cells, sitting on a basement
membrane and capped by a gelatinous cupula into which
the sensory bairs project. Neuromasts found on the supporting cells and mantle cells, sitting on a basement
membrane and capped by a gelatinous cupula into which
the sensory hairs project. Neuromasts found on the membrane and capped by a gelatinous cupula into which
the sensory hairs project. Neuromasts found on the
surface are called free or superficial neuromasts, and
these may be divided into at least two categories with the sensory hairs project. Neuromasts found on the surface are called free or superficial neuromasts, and these may be divided into at least two categories with different probable evolutionary origins (Coombs *et al*) surface are called free or superficial neuromasts, and
these may be divided into at least two categories with
different probable evolutionary origins (Coombs *et al.*
1988) Although elasmobranch pit organs have been identhese may be divided into at least two categories with
different probable evolutionary origins (Coombs *et al.*
1988). Although elasmobranch pit organs have been iden-
tified as free neuromasts (Tester & Nelson 1967; Beach different probable evolutionary origins (Coombs *et al.* ar
1988). Although elasmobranch pit organs have been iden-
tified as free neuromasts (Tester & Nelson 1967; Peach &
Rouse 2000) it is unclear which category they be 1988). Although elasmobranch pit organs have been identified as free neuromasts (Tester & Nelson 1967; Peach & Rouse 2000), it is unclear which category they belong to, or indeed whether they are functionally equivalent t tified as free neuromasts (Tester & Nelson 1967; Peach & Rouse 2000), it is unclear which category they belong to, or indeed whether they are functionally equivalent to the Rouse 2000), it is unclear which category they belong to,
or indeed whether they are functionally equivalent to the
free neuromasts of other vertebrates. The nomenclature of
free neuromasts is somewhat confused, with vario or indeed whether they are functionally equivalent to the
free neuromasts of other vertebrates. The nomenclature of
free neuromasts is somewhat confused, with various types
of free neuromasts, being described as 'pit organ free neuromasts of other vertebrates. The nomenclature of
free neuromasts is somewhat confused, with various types
of free neuromasts being described as 'pit organs' or
occurring in 'pit lines' (for further discussion of t free neuromasts is somewhat confused, with various types
of free neuromasts being described as 'pit organs' or
occurring in 'pit lines' (for further discussion of this issue see Coombs et al. (1988)). For the sake of clarity, 'pit

organs' will be used in this paper only to refer to the
organs of elasmobranchs, although the term may elseorgans' will be used in this paper only to refer to the organs of elasmobranchs, although the term may else-
where refer to free neuromasts in other vertebrates organs' will be used in this paper only to refer to
organs of elasmobranchs, although the term may
where refer to free neuromasts in other vertebrates.
Pit organs were initially called 'nervenbügel' or 's organs of elasmobranchs, although the term may else-
where refer to free neuromasts in other vertebrates.
Pit organs were initially called 'nervenhügel' or 'spalt-

where refer to free neuromasts in other vertebrates.
Pit organs were initially called 'nervenhügel' or 'spalt-
papillen'; the term 'pit organ' first appeared in the late
1800s, Various lateral-line researchers in the 19th Pit organs were initially called 'nervenhügel' or 'spalt-
papillen'; the term 'pit organ' first appeared in the late
1800s. Various lateral-line researchers in the 19th and
early 20th centuries (cited in Budker 1938) noted papillen'; the term 'pit organ' first appeared in the late 1800s. Various lateral-line researchers in the 19th and early 20th centuries (cited in Budker 1938) noted the existence of the pit organs and some made observation 1800s. Various lateral-line researchers in the 19th and early 20th centuries (cited in Budker 1938) noted the existence of the pit organs, and some made observations on their location innervation and/or histology In all o early 20th centuries (cited in Budker 1938) noted the existence of the pit organs, and some made observations
on their location, innervation and/or histology. In all of
these studies however the main focus was on the later existence of the pit organs, and some made observations
on their location, innervation and/or histology. In all of
these studies, however, the main focus was on the lateral-
line canal organs. Budker (1938) was the first t on their location, innervation and/or histology. In all of these studies, however, the main focus was on the lateral-
line canal organs. Budker (1938) was the first to attempt a synthesis of knowledge of the pit organs (' line canal organs. Budker (1938) was the first to attempt a ielles'), and to illustrate the generalized distribution of pit organs over the body surface of a shark. Budker's diagram of a cross- section through a pit organ showed organs over the body surface of a shark. Budker's
diagram of a cross-section through a pit organ showed
sensory cells reaching all the way from the apical surface
to the basement membrane, a characteristic of vertebrate diagram of a cross-section through a pit organ showed
sensory cells reaching all the way from the apical surface
to the basement membrane, a characteristic of vertebrate
taste buds. Budker also reported some experiments wh sensory cells reaching all the way from the apical surface
to the basement membrane, a characteristic of vertebrate
taste buds. Budker also reported some experiments where
fish-meat extract applied to the pit organs elicit to the basement membrane, a characteristic of vertebrate
taste buds. Budker also reported some experiments where
fish-meat extract applied to the pit organs elicited beha-
vioural responses. Given this evidence. Budker sug taste buds. Budker also reported some experiments where
fish-meat extract applied to the pit organs elicited beha-
vioural responses. Given this evidence, Budker suggested
that the pit organs had a gustatory function fish-meat extract applied to the pit organs elivioural responses. Given this evidence, Budke
that the pit organs had a gustatory function.
Interest in pit organs was revived in the vioural responses. Given this evidence, Budker suggested
that the pit organs had a gustatory function.
Interest in pit organs was revived in the late 1960s

that the pit organs had a gustatory function.
Interest in pit organs was revived in the late 1960s
when Tester & Nelson (1967) mapped the distribution of
pit organs on 15 species of sharks, and also examined Interest in pit organs was revived in the late 1960s
when Tester & Nelson (1967) mapped the distribution of
pit organs on 15 species of sharks, and also examined
their morphology and histology Like Budker they recogwhen Tester & Nelson (1967) mapped the distribution of
pit organs on 15 species of sharks, and also examined
their morphology and histology. Like Budker, they recog-
nized several distinct groups of pit organs—the most pit organs on 15 species of sharks, and also examined
their morphology and histology. Like Budker, they recog-
nized several distinct groups of pit organs—the most
numerous on the dorsolateral and lateral surfaces, a pair nized several distinct groups of pit organs—the most nized several distinct groups of pit organs—the most
numerous on the dorsolateral and lateral surfaces, a pair
anterior to each endolymphatic pore, a mandibular group
and an umbilical group. They noted that the pattern of numerous on the dorsolateral and lateral surfaces, a pair
anterior to each endolymphatic pore, a mandibular group
and an umbilical group. They noted that the pattern of
pit erran distribution varied among species, and some anterior to each endolymphatic pore, a mandibular group
and an umbilical group. They noted that the pattern of
pit organ distribution varied among species, and some-
times one or more of the groups was absent and an umbilical group. They noted that th
pit organ distribution varied among species,
times one or more of the groups was absent.
Based on their light microscopical observa Example is triangular varied among species, and some-
the some or more of the groups was absent.
Based on their light microscopical observations, Tester
Nelson (1967) were fairly certain that the nit organs

times one or more of the groups was absent.
Based on their light microscopical observations, Tester & Nelson (1967) were fairly certain that the pit organs Based on their light microscopical observations, Tester & Nelson (1967) were fairly certain that the pit organs
were ordinary free neuromasts, not external taste buds.
They observed that the sensory cells did not reach all & Nelson (1967) were fairly certain that the pit organs
were ordinary free neuromasts, not external taste buds.
They observed that the sensory cells did not reach all the
way to the basement membrane as Budker had claimed were ordinary free neuromasts, not external taste buds.
They observed that the sensory cells did not reach all the
way to the basement membrane as Budker had claimed,
and that the sensory cells appeared to bear apical bair They observed that the sensory cells did not reach all the way to the basement membrane as Budker had claimed, and that the sensory cells appeared to bear apical hairs way to the basement membrane as Budker had claimed,
and that the sensory cells appeared to bear apical hairs
extending into a cupula-like body, unlike the cells of taste
buds. They, were unable to adequately visualize the and that the sensory cells appeared to bear apical hairs
extending into a cupula-like body, unlike the cells of taste
buds. They were unable to adequately visualize the
cupula however despite trying a number of methods extending into a cupula-like body, unlike the cells of taste
buds. They were unable to adequately visualize the
cupula, however, despite trying a number of methods.

Figure 1. Pit organ of the stingray *Pastinachus sephen*.
Arrowhead indicates edge of neuromast. Scale bar, 100 µm.

Soon afterwards Tester & Kendall (1967) examined the Soon afterwards Tester & Kendall (1967) examined the
innervation of pit organs in two species of sharks. Like
earlier researchers who had focused on the lateral-line Soon afterwards Tester & Kendall (1967) examined the
innervation of pit organs in two species of sharks. Like
earlier researchers who had focused on the lateral-line
canals (e.g. Johnson 1917) they found that the innervat innervation of pit organs in two species of sharks. Like
earlier researchers who had focused on the lateral-line
canals (e.g. Johnson 1917), they found that the innervation
of the pit organs was intimately associated with earlier researchers who had focused on the lateral-line
canals (e.g. Johnson 1917), they found that the innervation
of the pit organs was intimately associated with that of
the canal neuromasts canals (e.g. Johnson 1917), they found that the innervation
of the pit organs was intimately associated with that of
the canal neuromasts.

Shortly afterwards, Katsuki *et al.* (1969) published the the canal neuromasts.
Shortly afterwards, Katsuki *et al.* (1969) published the
results of their electrophysiological experiments to investi-
gate the possible gustatory function of pit organs. They Shortly afterwards, Katsuki *et al.* (1969) published the results of their electrophysiological experiments to investigate the possible gustatory function of pit organs. They recorded responses to various jons a mechanical results of their electrophysiological experiments to investigate the possible gustatory function of pit organs. They recorded responses to various ions, a mechanical stimulus, and to substances that stimulate the taste bud gate the possible gustatory function of pit organs. They
recorded responses to various ions, a mechanical stimulus,
and to substances that stimulate the taste buds of
mammals. They reported that the pit organs responded recorded responses to various ions, a mechanical stimulus,
and to substances that stimulate the taste buds of
mammals. They reported that the pit organs responded
quite differently from the canal neuromasts to many of and to substances that stimulate the taste buds of mammals. They reported that the pit organs responded quite differently from the canal neuromasts to many of mammals. They reported that the pit organs responded might be.
quite differently from the canal neuromasts to many of The nathese stimuli, but their results were more qualitative than long par quite differently from the canal neuromasts to many of
these stimuli, but their results were more qualitative than
quantitative, and did little to clarify the functional
properties of pit organs. The mechanical stimulus th these stimuli, but their results were more qualitative than
quantitative, and did little to clarify the functional
properties of pit organs. The mechanical stimulus they
used although unclear was described as 'touch' and t quantitative, and did little to clarify the functional
properties of pit organs. The mechanical stimulus they
used, although unclear, was described as 'touch', and their
method for distinguishing pit organ and canal perves properties of pit organs. The mechanical stimulus they used, although unclear, was described as 'touch', and their method for distinguishing pit organ and canal nerves seems to have been somewhat unreliable. In addition th used, although unclear, was described as 'touch', and their
method for distinguishing pit organ and canal nerves
seems to have been somewhat unreliable. In addition, the
chemical stimuli they used may have been confounded method for distinguishing pit organ and canal nerves
seems to have been somewhat unreliable. In addition, the
chemical stimuli they used may have been confounded by
mechanical stimuli as the organs were 'flooded' with seems to have been somewhat unreliable. In addition, the organs appeared similar to canal neuromasts, it was only
chemical stimuli they used may have been confounded by recently that the morphology of pit organs was fully
 chemical stimuli they used may have been confounded by
mechanical stimuli as the organs were 'flooded' with
solutions (again, the exact method was unclear). They
concluded that nit organs were more sensitive to changes mechanical stimuli as the organs were 'flooded' with
solutions (again, the exact method was unclear). They
concluded that pit organs were more sensitive to changes
in salinity and cation concentrations and less sensitive t solutions (again, the exact method was unclear). They concluded that pit organs were more sensitive to changes
in salinity and cation concentrations, and less sensitive to
mechanical stimulation, than canal neuromasts. As concluded that pit organs were more sensitive to changes
in salinity and cation concentrations, and less sensitive to
mechanical stimulation, than canal neuromasts. As the
responses to salinity changes seemed especially ma in salinity and cation concentrations, and less sensitive to mechanical stimulation, than canal neuromasts. As the responses to salinity changes seemed especially marked, they speculated that the pit organs might function as salinity detectors responses to salinity
they speculated the
salinity detectors.
Katsuki & Hash ey speculated that the pit organs might function as
inity detectors.
Katsuki & Hashimoto (1969) did some further experi-
ents on the enhancement of mechanosensitivity in pit

salinity detectors.
Katsuki & Hashimoto (1969) did some further experiments on the enhancement of mechanosensitivity in pit
organs by potassium ions. They speculated that the lack Katsuki & Hashimoto (1969) did some further experiments on the enhancement of mechanosensitivity in pit organs by potassium ions. They speculated that the lack of a conventional cupula (as suggested by Tester $\&$ organs by potassium ions. They speculated that the lack
of a conventional cupula (as suggested by Tester &
Nelson) might account for the marked chemosensitivity of
pit organs. They also observed that the pit organ perves of a conventional cupula (as suggested by Tester &
Nelson) might account for the marked chemosensitivity of
pit organs. They also observed that the pit organ nerves
sometimes showed burst discharges synchronized with the Nelson) might account for the marked chemosensitivity of
pit organs. They also observed that the pit organ nerves
sometimes showed burst discharges synchronized with the
respiratory gill movements, as well as exhibiting sp pit organs. They also observed that the pit organ nerves
sometimes showed burst discharges synchronized with the
respiratory gill movements, as well as exhibiting spontasometimes showed burst discharges synchronized with the
respiratory gill movements, as well as exhibiting sponta-
neous activity. Evidence was mounting that the pit organs
had similar, functions, to other lateral-line orga respiratory gill movements, as well as exhibiting spontaneous activity. Evidence was mounting that the pit organs
had similar functions to other lateral-line organs, but
Katsuki & Hashimoto (1969) apparently considered tha neous activity. Evidence was mounting that the pit organs
had similar functions to other lateral-line organs, but
Katsuki & Hashimoto (1969) apparently considered that Katsuki & Hashimoto (1969) apparently considered that *Phil. Trans. R. Soc. Lond.* B (2000)

Figure 2. Two large modified denticles covering the pit organ of the epaulette shark *Hemiscyllium ocellatum*. Scale bar, $100 \,\mathrm{\upmu m}$.

100 μ m.
their chemoreceptivity was functionally significant, rather
than just a by-product of receptor physiology their chemoreceptivity was functionally signific
than just a by-product of receptor physiology.
After Tester & Nelson's (1967) paper, the eir chemoreceptivity was functionally significant, rather
an just a by-product of receptor physiology.
After Tester & Nelson's (1967) paper, the hypothesis
at pit organs were ordinary free neuromasts received

than just a by-product of receptor physiology.

After Tester & Nelson's (1967) paper, the hypothesis

that pit organs were ordinary free neuromasts received

fairly wide acceptance in the scientific community Specu-After Tester & Nelson's (1967) paper, the hypothesis
that pit organs were ordinary free neuromasts received
fairly wide acceptance in the scientific community. Specu-
lation that pit organs were taste buds, however, still that pit organs were ordinary free neuromasts received
fairly wide acceptance in the scientific community. Specu-
lation that pit organs were taste buds, however, still fairly wide acceptance in the scientific community. Speculation that pit organs were taste buds, however, still appeared from time to time in popular literature. The conclusions of Katsuki and his colleagues that the pit lation that pit organs were taste buds, however, still
appeared from time to time in popular literature. The
conclusions of Katsuki and his colleagues that the pit
organs had a chemorecentive function perhaps lent some appeared from time to time in popular literature. The
conclusions of Katsuki and his colleagues that the pit
organs had a chemoreceptive function perhaps lent some
resilience to Budker's theory. In an echo of Budker's conclusions of Katsuki and his colleagues that the pit
organs had a chemoreceptive function perhaps lent some
resilience to Budker's theory. In an echo of Budker's organs had a chemoreceptive function perhaps lent some
resilience to Budker's theory. In an echo of Budker's
behavioural experiment, Katsuki *et al.* (1969) found that
the pit organs of sharks showed dramatic neural respon resilience to Budker's theory. In an echo of Budker's
behavioural experiment, Katsuki *et al.* (1969) found that
the pit organs of sharks showed dramatic neural responses
to the application of meat or blood. Although the w behavioural experiment, Katsuki *et al.* (1969) found that
the pit organs of sharks showed dramatic neural responses
to the application of meat or blood. Although the words
'blood' and 'shark' together in a sentence may be the pit organs of sharks showed dramatic neural responses
to the application of meat or blood. Although the words
'blood' and 'shark' together in a sentence may be evoca-
tive, it is difficult to imagine of what behavioura to the application of meat or blood. Although the words 'blood' and 'shark' together in a sentence may be evoca-

The nature of pit organs remained uncertain for so long partly because their structure had only been documented using the light microscope, which did not long partly because their structure had only been
documented using the light microscope, which did not
provide sufficient resolution to determine whether they
were typical neuromasts. Although Hama & Yamada documented using the light microscope, which did not
provide sufficient resolution to determine whether they
were typical neuromasts. Although Hama & Yamada
(1977) mentioned unpublished data indicating that the pit provide sufficient resolution to determine whether they
were typical neuromasts. Although Hama & Yamada
(1977) mentioned unpublished data indicating that the pit
organs appeared similar to canal neuromasts it was only were typical neuromasts. Although Hama & Yamada
(1977) mentioned unpublished data indicating that the pit
organs appeared similar to canal neuromasts, it was only
recently, that the morphology of pit organs was fully (1977) mentioned unpublished data indicating that the pit organs appeared similar to canal neuromasts, it was only recently that the morphology of pit organs was fully investigated at the electron microscope level (Peach organs appeared similar to canal neuromasts, it was only recently that the morphology of pit organs was fully
investigated at the electron microscope level (Peach &
Rouse 2000). We have now documented the morphology
of the pit organs of a variety of elasmobranch species investigated at the electron microscope level (Peach & Rouse 2000). We have now documented the morphology of the pit organs of a variety of elasmobranch species, confirming that in most respects they have the structure Rouse 2000). We have now documented the morphology
of the pit organs of a variety of elasmobranch species,
confirming that in most respects they have the structure
of typical neuromasts (Peach & Marshall 2000) of the pit organs of a variety of elasmobranch species, confirming that in most respects they have the structure of typical neuromasts (Peach & Marshall 2000).

2. RESULTS AND DISCUSSION

ments on the enhancement of mechanosensitivity in pit with the naked eye, due to their association with organs by potassium ions. They speculated that the lack enlarged and modified placoid scales (denticles), with of a co The pit organs of some elasmobranchs can be detected **EXEMPLE AND DISCUSSION**
The pit organs of some elasmobranchs can be detected
with the naked eye, due to their association with
enlarged and modified placoid scales (denticles) with The pit organs of some elasmobranchs can be detected
with the naked eye, due to their association with
enlarged and modified placoid scales (denticles), with
growes in the skin, or sometimes (Mustelus antarcticus with the naked eye, due to their association with
enlarged and modified placoid scales (denticles), with
grooves in the skin, or sometimes (*Mustelus antarcticus*
and *Etmohterus* spp) with distinct patterns of pigmentaenlarged and modified placoid scales (denticles), with
grooves in the skin, or sometimes (*Mustelus antarcticus*
and *Etmopterus* spp.) with distinct patterns of pigmenta-
tion (Budker 1938: Reif 1985: M_B_Peach and N_I grooves in the skin, or sometimes (*Mustelus antarcticus* and *Etmopterus* spp.) with distinct patterns of pigmentation (Budker 1938; Reif 1985; M. B. Peach and N. J. Marshall unpublished data). The functional significance and *Etmopterus* spp.) with distinct patterns of pigmentation (Budker 1938; Reif 1985; M. B. Peach and N. J. Marshall, unpublished data). The functional significance of these accessory structures is unclear but possibly tion (Budker 1938; Reif 1985; M. B. Peach and N. J. Marshall, unpublished data). The functional significance of these accessory structures is unclear, but possibly Marshall, unpublished data). The functional significance
of these accessory structures is unclear, but possibly
includes protection against abrasion or direction of water
flow towards the sensory surface. The few rays so f of these accessory structures is unclear, but possibly
includes protection against abrasion or direction of water
flow towards the sensory surface. The few rays so far
documented have their pit organs located within includes protection against abrasion or direction of water
flow towards the sensory surface. The few rays so far
documented have their pit organs located within

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Figure 3. Pit organ of the shovelnose ray *Rhinobatos typus*.
Arrowhead indicates edge of neuromast. Scale bar, 100 µm.

grooves, and exposed to direct water flow, while the pit
organs of most sharks are covered by more or less grooves, and exposed to direct water flow, while the pit
organs of most sharks are covered by more or less
imbricate denticles (Budker 1938: Reif 1985: Maruska & grooves, and exposed to direct water flow, while the pit
organs of most sharks are covered by more or less
imbricate denticles (Budker 1938; Reif 1985; Maruska & re
Tricas 1998) (figures 1 and 2) Although these denticles organs of most sharks are covered by more or less
imbricate denticles (Budker 1938; Reif 1985; Maruska &
Tricas 1998) (figures 1 and 2). Although these denticles
clearly have some effect on the hydrodynamic environimbricate denticles (Budker 1938; Reif 1985; Maruska & Tricas 1998) (figures 1 and 2). Although these denticles
clearly have some effect on the hydrodynamic environ-
ment of the pit organ water flow around and under-Tricas 1998) (figures 1 and 2). Although these denticles
clearly have some effect on the hydrodynamic environ-
ment of the pit organ, water flow around and under-
neath them has yet to be modelled clearly have some effect on the hydrodynamic environ-
ment of the pit organ, water flow around and under-
neath them has yet to be modelled.
A few sluggish, mainly bottom-dwelling sharks (the ent of the pit organ, water flow around and under-
ath them has yet to be modelled.
A few sluggish, mainly bottom-dwelling sharks (the
sel shark *Squating*, the lantern shark *Etmohterus*, the

angel shark *Squatina*, the lantern shark *Etmopterus*, the A few sluggish, mainly bottom-dwelling sharks (the angel shark *Squatina*, the lantern shark *Etmopterus*, the sevengill shark *Notorhynchus*, the sawfish *Pristis* and saw-shark *Pristiohhorus*) are known to have pit orga angel shark *Squatina*, the lantern shark *Etmopterus*, the sevengill shark *Notorhynchus*, the sawfish *Pristis* and sawshark *Pristiophorus*) are known to have pit organs in grooves like those of rays (Daniel 1934: Budke sevengill shark *Notorhynchus*, the sawfish *Pristis* and sawshark *Pristiophorus*) are known to have pit organs in grooves, like those of rays (Daniel 1934; Budker 1938; Reif 1985) In some of these sharks the pit organs a shark *Pristiophorus*) are known to have pit organs in grooves, like those of rays (Daniel 1934; Budker 1938; Reif 1985). In some of these sharks, the pit organs are also grooves, like those of rays (Daniel 1934; Budker 1938; Reif 1985). In some of these sharks, the pit organs are also associated with modified denticles nearby, although these do not usually cover the pit organs. The showeln 1985). In some of these sharks, the pit organs are also
associated with modified denticles nearby, although these
do not usually cover the pit organs. The shovelnose ray
Rhinobatos and the guitar-fish *Rhynchobatus*, als do not usually cover the pit organs. The shovelnose ray *Rhinobatos* and the guitar-fish *Rhynchobatus* also have do not usually cover the pit organs. The shovelnose ray
Rhinobatos and the guitar-fish *Rhynchobatus* also have
modified denticles adjacent to their pit organ grooves
(figure 3) Although these data suggest that exposed p *Rhinobatos* and the guitar-fish *Rhynchobatus* also have
modified denticles adjacent to their pit organ grooves
(figure 3). Although these data suggest that exposed pit
organs in grooves are related to a hottom-dwelling l modified denticles adjacent to their pit organ grooves
(figure 3). Although these data suggest that exposed pit
organs in grooves are related to a bottom-dwelling life-
style more typical pit organs covered by imbricate (figure 3). Although these data suggest that exposed pit organs in grooves are related to a bottom-dwelling life-
style, more typical pit organs covered by imbricate organs in grooves are related to a bottom-dwelling life-
style, more typical pit organs covered by imbricate
denticles have been recorded on other bottom-dwelling
and demersal sharks (e.g. Hemicallium Ginglamastama and style, more typical pit organs covered by imbricate
denticles have been recorded on other bottom-dwelling
and demersal sharks (e.g. *Hemiscyllium*, *Ginglymostoma* and
Mustelus) Thus the morphology of the pit organs and denticles have been recorded on other bottom-dwelling
and demersal sharks (e.g. *Hemiscyllium, Ginglymostoma* and
Mustelus). Thus the morphology of the pit organs and
their accessory structures may relate more strongly t and demersal sharks (e.g. *Hemiscyllium*, *Ginglymostoma* and *Mustelus*). Thus the morphology of the pit organs and their accessory structures may relate more strongly to *Mustelus*). Thus the morphology of the pit organs and
their accessory structures may relate more strongly to
phylogeny than to ecology. In some other sharks
(Chlamydoselachus Eutentamicrus Isistius Echinothinus and (*Chlamydoselachus*, *Eup rotomicrus*, *Isistius*, *Echinorhinus* and phylogeny than to ecology. In some other sharks (*Chlamydoselachus*, *Eup rotomicrus*, *Isistius*, *Echinorhinus* and *Mitsukurina*) the pit organs have not yet been located, as there is no modification of the denticles or (Chlamydoselachus, Eup rotomicrus, Isistius, Echinorhinus and Mitsukurina) the pit organs have not yet been located, as there is no modification of the denticles or skin to indicate their presence (Reif 1985) *Mitsukurina*) the pit organs l
there is no modification of the
their presence (Reif 1985).
The number of pit organ Exercis no modification of the denticles or skin to indicate

eir presence (Reif 1985).

The number of pit organs appears to remain constant

ring optogeny but may vary among conspecific

their presence (Reif 1985).
The number of pit organs appears to remain constant
during ontogeny, but may vary among conspecific
individuals as well as among species (Tester & Nelson The number of pit organs appears to remain constant
during ontogeny, but may vary among conspecific
individuals as well as among species (Tester & Nelson
1967) The number of pit organs on one side of the body during ontogeny, but may vary among conspecific
individuals as well as among species (Tester & Nelson
1967). The number of pit organs on one side of the body
ranges from about 77 in $(1\text{in} - 0.025\text{m})$. Squalus acanthia individuals as well as among species (Tester & Nelson
1967). The number of pit organs on one side of the body
ranges from about 77 in (1in = 0.025 m) *Squalus acanthias*
to over 600 in *Shhyrna levini* (Tester & Nelson 196 1967). The number of pit organs on one side of the body
ranges from about 77 in $(1\text{in} = 0.025 \text{m})$ *Squalus acanthias*
to over 600 in *Sphyrna lewini* (Tester & Nelson 1967). The
nit organs of rays are apparently less n ranges from about 77 in $(1\text{in} = 0.025 \text{m})$ *Squalus acanthias* to over 600 in *Sphyrna lewini* (Tester & Nelson 1967). The pit organs of rays are apparently less numerous than those of sharks (Budker 1938) but their distribution has been pit organs of rays are apparently less numerous than those
of sharks (Budker 1938) but their distribution has been
completely documented only for *Dasyatis sabina* (Maruska
& Tricas 1997) and *Rhinghatas tybus* (Peach & Ma of sharks (Budker 1938) but their distribution has been
completely documented only for *Dasyatis sabina* (Maruska
& Tricas 1997) and *Rhinobatos typus* (Peach & Marshall
2000) Because the data set is fairly small and inclu completely documented only for *Dasyatis sabina* (Maruska & Tricas 1997) and *Rhinobatos typus* (Peach & Marshall 2000). Because the data set is fairly small and includes mainly pelagic sharks, relationships between pit or & Tricas 1997) and *Rhinobatos typus* (Peach & Marshall 2000). Because the data set is fairly small and includes mainly pelagic sharks, relationships between pit organ

abundance and phylogeny or ecology are difficult to
discern Reif (1985) however did note a positive correlaabundance and phylogeny or ecology are difficult to
discern. Reif (1985), however, did note a positive correla-
tion between pit organ abundance and swimming speed discern. Reif (1985), however, did note a positive correlation between pit organ abundance and swimming speed in sharks. tion between pit organ abundance and swimming speed In between pit organ abundance and swimming speed
sharks.
The behavioural role of pit organs remains mysterious.
ster & Nelson (1967) suggested that they may play a

in sharks.
The behavioural role of pit organs remains mysterious.
Tester & Nelson (1967) suggested that they may play a
role in prev capture under dim light conditions, while Tester & Nelson (1967) suggested that they may play a role in prey capture under dim light conditions, while Katsuki and his colleagues focused on their chemorole in prey capture under dim light conditions, while
Katsuki and his colleagues focused on their chemo-
receptive properties and suggested that they may be
detectors of salinity changes. This seems unlikely as very Katsuki and his colleagues focused on their chemo-
receptive properties and suggested that they may be
detectors of salinity changes. This seems unlikely, as very
few elasmobranch species migrate between salt and fresh receptive properties and suggested that they may be
detectors of salinity changes. This seems unlikely, as very
few elasmobranch species migrate between salt and fresh
water although most if not all elasmobranchs possess p detectors of salinity changes. This seems unlikely, as very
few elasmobranch species migrate between salt and fresh
water, although most if not all elasmobranchs possess pit
organs. Reif (1985) suggested that the pit organ few elasmobranch species migrate between salt and fresh
water, although most if not all elasmobranchs possess pit
organs. Reif (1985) suggested that the pit organs might
function as detectors of swimming speed. This seems water, although most if not all elasmobranchs possess pit
organs. Reif (1985) suggested that the pit organs might
function as detectors of swimming speed. This seems
feasible as the free neuromasts of other fishes and amph organs. Reif (1985) suggested that the pit organs might
function as detectors of swimming speed. This seems
feasible, as the free neuromasts of other fishes and amphi-
bians are directly exposed to water motion, and detect function as detectors of swimming speed. This seems
feasible, as the free neuromasts of other fishes and amphi-
bians are directly exposed to water motion, and detect
velocity (citations in Blaxter 1987). It is not yet cle feasible, as the free neuromasts of other fishes and amphibians are directly exposed to water motion, and detect velocity (citations in Blaxter 1987). It is not yet clear, however, whether the pit organs of sharks, for the bians are directly exposed to water motion, and detect
velocity (citations in Blaxter 1987). It is not yet clear,
however, whether the pit organs of sharks, for the most
part well shielded by overlying denticles receive th velocity (citations in Blaxter 1987). It is not yet clear,
however, whether the pit organs of sharks, for the most
part well shielded by overlying denticles, receive the same
kind of stimuli as the free neuromasts of other however, whether the pit organs of sharks, for the most
part well shielded by overlying denticles, receive the same
kind of stimuli as the free neuromasts of other vertebrates.
Maruska & Tricas (1998) noted that the pit or part well shielded by overlying denticles, receive the same
kind of stimuli as the free neuromasts of other vertebrates.
Maruska & Tricas (1998) noted that the pit organs of
stingrays were well placed to detect water movem kind of stimuli as the free neuromasts of other vertebrates.
Maruska & Tricas (1998) noted that the pit organs of stingrays were well placed to detect water movements generated by tidal currents, conspecifics or predators. Ironically were well placed to detect water movements

Ironically, it seems to have been clear to the earliest

Ironically, it seems to have been clear to the earliest

Ironically, it seems to have been clear to the earlie

generated by tidal currents, conspecifics or predators.
Ironically, it seems to have been clear to the earliest
researchers that the pit organs belonged within the
lateral-line system. The influential work of Budker Ironically, it seems to have been clear to the earliest
researchers that the pit organs belonged within the
lateral-line system. The influential work of Budker
initiated the confusion that has persisted until recently. A researchers that the pit organs belonged within the lateral-line system. The influential work of Budker initiated the confusion that has persisted until recently. A number of annroaches can now be taken to improving lateral-line system. The influential work of Budker
initiated the confusion that has persisted until recently. A
number of approaches can now be taken to improving
our understanding of pit organs. Electrophysiological initiated the confusion that has persisted until recently. A
number of approaches can now be taken to improving
our understanding of pit organs. Electrophysiological
recordings from the pit organ perves in the presence of number of approaches can now be taken to improving
our understanding of pit organs. Electrophysiological
recordings from the pit organ nerves, in the presence of
controlled mechanical stimuli could establish whether our understanding of pit organs. Electrophysiological
recordings from the pit organ nerves, in the presence of
controlled mechanical stimuli, could establish whether
the pit organs have frequency response characteristics recordings from the pit organ nerves, in the presence of
controlled mechanical stimuli, could establish whether
the pit organs have frequency response characteristics
similar to those of the free neuromasts of other vertecontrolled mechanical stimuli, could establish whether
the pit organs have frequency response characteristics
similar to those of the free neuromasts of other verte-
brates Behavioural experiments where the pit organs are the pit organs have frequency response characteristics
similar to those of the free neuromasts of other verte-
brates. Behavioural experiments, where the pit organs are
occluded by chemical or mechanical means, could deter similar to those of the free neuromasts of other verte-
brates. Behavioural experiments, where the pit organs are
occluded by chemical or mechanical means, could deter-
mine whether the pit organs are important in rheotaxi brates. Behavioural experiments, where the pit organs are or prey detection. Modelling of the immediate hydrodynamic environment of the pit organs, and how this is or prey detection. Modelling of the immediate hydrodynamic environment of the pit organs, and how this is affected by the accessory structures, would help to clarify the relevant stimulus. Work is currently under way to dynamic environment of the pit organs, and how this is
affected by the accessory structures, would help to clarify
the relevant stimulus. Work is currently under way to
document the distribution and morphology of pit organ affected by the accessory structures, would help to clarify
the relevant stimulus. Work is currently under way to
document the distribution and morphology of pit organs
on more species of elasmobranchs especially bottom the relevant stimulus. Work is currently under way to
document the distribution and morphology of pit organs
on more species of elasmobranchs, especially bottom
dwellers (Peach & Marshall 2000) document the distribution and morp
on more species of elasmobranchs
dwellers (Peach & Marshall 2000). dwellers (Peach & Marshall 2000).
Most specimens were collected at Heron Island Research

Most specimens were collected at Heron Island Research
Station, on the Great Barrier Reef, Australia. Gillian Renshaw,
Veronica Soderström and Mike Bennett also donated elasmo-Most specimens were collected at Heron Island Research
Station, on the Great Barrier Reef, Australia. Gillian Renshaw,
Veronica Soderström and Mike Bennett also donated elasmo-
branch skin specimens Malcolm Iones provided Station, on the Great Barrier Reef, Australia. Gillian Renshaw,
Veronica Soderström and Mike Bennett also donated elasmo-
branch skin specimens. Malcolm Jones provided assistance with
electron microscopy at the Centre for Veronica Soderström and Mike Bennett also donated elasmo-
branch skin specimens. Malcolm Jones provided assistance with
electron microscopy, at the Centre for Microscopy and Micro-
analysis. University of Queensland. The a branch skin specimens. Malcolm Jones provided assistance with
electron microscopy, at the Centre for Microscopy and Micro-
analysis, University of Queensland. The authors benefited from
discussions with many lateral-line r electron microscopy, at the Centre for Microscopy and Micro-
analysis, University of Queensland. The authors benefited from
discussions with many lateral-line researchers, including Tim
Tricas, Sheryl Coombs, John Montgome analysis, University of Queensland. The authors benefited from
discussions with many lateral-line researchers, including Tim
Tricas, Sheryl Coombs, John Montgomery, John New, Jacqueline
Webb, Horst Bleckmann and Ad Kalmiin discussions with many lateral-line researc
Tricas, Sheryl Coombs, John Montgomery, J
Webb, Horst Bleckmann and Ad Kalmijn.

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