Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living supraspecific taxa of Chondrichthyan fishes

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by J. HERMAN, M. HOVESTADT-EULER, D.C. HOVESTADT & M. STEHMANN
the Torpediniformes into two families: the Torpedinidae and Narcinidae. He subdivided further the Torpedinidae into the subfamilies Torpedininae, with the genus *Torpedo*, and Hypnininae, with the genus *Hypnos*. Gill (1862) subdivided the genus *Torpedo* into two subgenera: *T. (Torpedo)* and *T. (Tetronarke)*. The tooth morphology of representatives of both subgenera will be described, illustrated and compared, additionally. Nelson (1994) also subdivided the Narcinidae into the two subfamilies Narcininae, with the genera *Benthobatis*, *Diplobatis*, *Discopyge* and *Narcine*, and Narkinae, with the genera *Crassinarke*, *Heteronarke*, *Narke*, *Temera* and *Typhlonarke*. The nominal species listed of each genus or subgenus are after MOULD (1999).

Cappetta (1988, along with the description and illustration of a new fossil torpediniform taxon based on tooth morphology, also described and illustrated the tooth morphology of most of the extant genera. The taxa are here redescribed and illustrated by SEM-photographs according to the standard of this series, with additional information about the tooth vascularization.

A differential diagnosis and conclusions on the classification of the torpediniformes are given from the odontological point of view. However, being aware of dealing with one complex of characters only, the odontological results will be presented here only, and we leave it to following revising authors to incorporate also odontological points of view in a full systematic review with eventual possible taxonomic and nomenclatural changes. The complete bibliographical reference for each genus, subgenus and species here described will be given in the descriptive section, respectively, and not be repeated under literature references. Along with every description of the tooth morphology, the vascularization of the teeth will be described and illustrated.

**Material**

The following 61 species of 17 genera and 2 subgenera were examined for this study:

- **Bengalichthys impennis**
  - Coll. Herman  ♂ 160 mm TL

- **Benthobatis moreshyi**
  - Coll. Herman  ♂ 215 mm TL

- **Crassinarke dormitor**
  - UMTF 20718  ♂ 190 mm TL

- **Diplobatis ommata**
  - Coll. Herman ♀ 250 mm TL
  - MNHN uncat. ♀ 150 mm TL

- **Discopyge tschudii**
  - ISH 883-1979  ♂ 357 mm TL
  - Coll. Herman  ♂ 400 mm TL
  - ISH 1632-1966 ♀ 165 mm TL
  - ISH 1632-1966 ♀ 307 mm TL

- **Heteronarce garmani**
  - ISH 225-1975 ♀ 219 mm TL

- **Heteronarce mollis**
  - ISH 254-1975 ♂ 196 mm TL

- **Hypnos monopterigium**
  - Coll. Hartman ♀ 265 mm TL

- **Hypnos subnigrum**
  - Coll. Herman ♂ 140 mm TL
  - Coll. Herman ♀ 270 mm TL

- **Narcine brasiliensis**
  - ISH 1856-1968 ♂ 249 mm TL
  - ISH 1856-1968 ♀ 540 mm TL

- **Narke dipterygia**
  - Coll. Herman ♀ 160 mm TL
  - ISH 8-1961 ♀ 163 mm TL

- **Temera hardwicki**
  - Coll. Herman ♂ 105 mm TL

- **Torpedo (Tetronarke) sp.**
  - Coll. Herman ♂ 253 mm TL
  - Coll. Herman ♂ 310 mm TL
  - Coll. Herman ♂ 315 mm TL
  - Coll. Herman ♂ 340 mm TL
  - Coll. Herman ♂ 3 mm TL
  - Coll. Herman ♀ 328 mm TL
  - Coll. Herman ♀ 340 mm TL
  - Coll. Herman ♀ 3 mm TL

- **Torpedo (Tetronarke) nobiliana**
  - Coll. Hovestadt ♀ 620 mm TL
  - Coll. Hovestadt ♀ 800 mm TL
  - Coll. Hovestadt ♀ 890 mm TL
  - Coll. Hovestadt ♀ 1050 mm TL
  - Coll. Herman ♀ 3 mm TL

- **Torpedo (Torpedo) torpedo**
  - Coll. Herman ♂ 350 mm TL
  - Coll. Herman ♂ 350 mm TL
  - Coll. Herman ♂ 380 mm TL
  - Coll. Herman ♂ 380 mm TL
  - Coll. Herman ♂ 385 mm TL
  - Coll. Herman ♂ 405 mm TL
  - Coll. Herman ♂ 410 mm TL
  - Coll. Herman ♂ 345 mm TL
  - Coll. Herman ♀ 360 mm TL

- **Torpedo (Torpedo) marmorata**
  - Coll. Hovestadt ♂ 150 mm TL
  - Coll. Hovestadt ♂ 160 mm TL
  - Coll. Hovestadt ♂ 160 mm TL
  - Coll. Hovestadt ♂ 190 mm TL
Coll. Herman ♂ 385 mm TL
Coll. Hovestadt ♀ 120 mm TL
Coll. Hovestadt ♀ 185 mm TL
Coll. Hovestadt ♀ 250 mm TL
Coll. Hovestadt ♀ 260 mm TL
Coll. Hovestadt ♀ 290 mm TL
Coll. Herman ♀ 350 mm TL
Coll. Hovestadt ♀ 360 mm TL
Coll. Hovestadt ♀ 370 mm TL
Coll. Herman ♀ 430 mm TL
Coll. Hovestadt ♀ 450 mm TL
Coll. Hovestadt ♀ 500 mm TL
Coll. Hovestadt ♀ 500 mm TL
Coll. Hovestadt ♀ 620 mm TL

Typhlonarke aaysoni
Coll. Herman ♂ 200 mm TL

Additionally, the illustrations of Cappetta (1988) were used.

**Description of the odontological characters**

**Family:** Narcinidae  
**Subfamily:** Narcinae

The Narcinidae comprise the genera *Benthobatis*, *Diplobatis*, *Discopyge* and *Narcine*.

**Genus:** *Benthobatis* Alcock, 1898


The genus comprises three named species: *B. Krefftii* (recently described by Rincon, Stehmann & Vooren, 2001), *B. marcida* and the type species *B. moresbyi*. A fourth, yet undescribed species from Taiwanese waters was mentioned by Carvalho (1999).

*Benthobatis moresbyi* Alcock, 1898  
(Plates: 1 and 2)

**HETERODONTY**

The dentition is gradient monognathic heterodont with lateral and posterior teeth becoming generally smaller and the cusp slightly more inclining toward the commissure. Lacking female and juvenile specimens sexual and ontogenetic heterodonty cannot be evaluated.

**VASCULARIZATION**

The teeth show the holaulacorhizid root type with an elongated, well developed pulp cavity, from which the vascular tubes of the circumpulpar dentine radiate into crown and root. Osteodentine and inner lateral foramina are absent. (See textfigure 1).

Textfigure 1. *Benthobatis* tooth histological cross section

**MALES AND FEMALES**

The crown is divided by sharp mesial and distal cutting edges into an inner and outer face. The outer face shows an arched, rounded crown base, largely overhanging the root. Both, mesial and distal cutting edges are of about equal size and arched similarly, each joining seamlessly with the crown base. In about the middle of the crown both cutting edges turn upward to form a narrow cusp, being half as high as the length of a cutting edge. The cusp becomes only slightly and gradually lower in lateral and posterior teeth. The outer surface is slightly concave. Generally, the smooth inner face is concave, but the mid-section is convex. Inner and outer ornamentation are absent.

The basal surface of the crown shows a rather, broad, slightly rounded crown rim at the outer margins, with inner and outer parts joining in blunt mesial and distal angles. The crown-root junction lies in a relatively deep depression in the center of the crown’s basal surface.

The high, narrow holaulacorhizid root is more or less oval in cross-section, slightly oblique toward the rear of the tooth, and slightly diverges at the root base. The root base presents a well-developed, deep and narrow median groove, with a relatively large aperture in the outer central base of the groove. Root coating is present at about one third of the upper part, all around the root. Inner and outer foramina are absent.

**Genus:** *Diplobatis* Bigelow & Schroeder, 1948


This genus comprises the species *D. colombiensis*, *D. guamachensis*, *D. pictus* and the type species *D. ommata*.

**Diplobatis ommata** (Jordan & Bollman, 1890)  
(Plates: 3 and 4)

**Discopyge ommata** Jordan & Bollman, 1890 Description of new species of fishes collected at the Galapagos Islands.

**HETERODONTY**

The dentition is gradient monognathic heterodont with lateral and posterior teeth becoming lower and the cusp tip slightly inclined toward the commissure. Sexual heterodonty is absent. Lacking juvenile material ontogenetic heterodonty cannot not be evaluated.

**VASCULARIZATION**

The teeth show the holaulacorhizid root type with an elongated, well developed pulp cavity, from which the vascular tubes of the circumpulpar dentine radiate into crown and root. Osteodentine and inner lateral foramina are absent. (See textfigure 2)

![Textfigure 2. Diplobatis tooth histological cross section](image1)

**MALES AND FEMALES**

The crown is divided by sharp mesial and distal cutting edges into an inner and outer face. The outer face shows an arched, convex crown base, more or less overhanging the root. Both, mesial and distal cutting edges are of about equal size and blade-like, each joining the crown base in a blunt angle. In about the middle part of the crown both cutting edges turn upward, after lowering as a blunt notch, to form a narrow, elongated cusp, about as high as the length of a cutting edge. The cusp becomes only slightly and gradually lower and more oblique distally in lateral and posterior teeth. The outer surface is slightly concave. Generally, the smooth inner face is concave, but the mid-section is convex. Inner and outer ornamentation are absent.

The basal surface of the crown shows a rather, broad, slightly rounded crown rim at the outer margins, with inner and outer parts joining in blunt mesial and distal angles. The crown-root junction lies in a relatively deep depression in the centre of the crown’s basal surface.

The narrow holaulacorhizid root is more or less oval in cross-section, slightly oblique toward the rear of the tooth, and diverges at the root base. The root base presents a well-developed, moderately broad, shallow median groove, with a relatively large aperture in the outer central base of the groove. Root coating is present at about one third of the upper part, all around the root. Inner and outer foramina are absent.

**Genus: Discopyge HECKEL, 1846**


The genus is monotypic with the type species *Discopyge tschudii*.

**Discopyge tschudii HECKEL, 1846**

(Plates: 5 to 9)

**Torpedo tschudii HENKEL, 1846 Ichthyologie. In: Tschudi 1846 Untersuchungen über die Fauna Peruana. Scheitlin & Zollikofer, St. Gallen. 1844-1846 in 12 parts Fauna Peru.**

**HETERODONTY**

The dentition is gradient monognathic heterodont with lateral and posterior teeth becoming lower and the cusp slightly inclined toward the commissure. Sexual heterodonty is absent. Ontogenetic heterodonty is presented by less developed, lower cutting edges and cusp in juveniles.

**VASCULARIZATION**

The teeth show the holaulacorhizid root type with an elongated, well developed pulp cavity, from which the vascular tubes of the circumpulpar dentine radiate into crown and root. Osteodentine and inner lateral foramina are absent. (See textfigure 3)

![Textfigure 3. Discopyge tooth histological cross section](image2)

**MALES AND FEMALES**

The crown is divided by sharp mesial and distal cutting edges into an inner and outer face. The outer face shows an arched, convex crown base, more or less overhanging the root. Both, mesial and distal cutting edges are of about equal size and blade-like, each joining the crown base in a blunt angle. In about the middle part of the crown both cutting edges turn upward, after lowering as a blunt notch, to form a narrow, elongated cusp being about as high as the length of a cutting edge. The cusp being only slightly and gradually lower in lateral and posterior teeth. The outer surface is slightly concave. Generally, the smooth inner face is concave, but the mid-section is convex. Inner and outer ornamentation are absent.

The basal surface of the crown shows a rather, broad, slightly rounded crown rim at the outer margins, with inner and outer parts joining in blunt mesial and distal angles. The crown-root junction lies in a relatively deep depression in the centre of the crown’s basal surface.
The high, narrow holaulacorhizid root is more or less oval in cross-section, slightly oblique toward the rear of the tooth, and diverges at the root base. The root base presents a well-developed, moderately broad, shallow median groove, with a relatively large aperture in the outer central base of the groove. Root coating is present at about one third of the upper part, all around the root. Inner and outer foramina are absent.

Genus: Narcine HENLE, 1834

The genus comprises the species N. bicolor, N. brasiliensis, N. brevilamia, N. brunnea, N. entemedor, N. firma, N. indica, N. lingula, N. maculata (type species), N. nigra, N. prodorsalis, N. rierai, N. tasmaniensis, N. timlei, N. verniculatus and N. westraliensis. Lacking tooth material of the type species N. brasiliensis was used instead for description and illustration.

Narcine brasiliensis (OLFERS, 1831) (Plates: 10 and 11)


HETERODONTY

The dentition is gradient monognathic heterodont with lateral and posterior teeth becoming lower and the cusp slightly inclined toward the commissure. Sexual heterodonty is absent. Ontogenetic heterodonty is presented by less developed, lower cutting edges and cusp in juveniles.

VASCULARIZATION

The teeth show the holaulacorhizid root type with an elongated, well developed pulp cavity, from which the vascular tubes of the circumpulpar dentine radiate into crown and root. Osteodentine and inner lateral foramina are absent. (See textfigure 4)

MALES AND FEMALES

The crown is divided by sharp mesial and distal cutting edges into an inner and outer face. The outer face shows an arched, rounded crown base, overhanging the root. Both, mesial and distal cutting edges are of about equal size and similarly arched, each joining seamlessly with the crown base. At about one third of the crown both cutting edges turn upward to form a cusp being half as high as the length of a cutting edge. The cusp becomes lower gradually and more oblique in lateral and posterior teeth. The outer surface is slightly concave. Generally, the smooth inner face is concave, but the mid-section is convex. Inner and outer ornamentation are absent. The basal surface of the crown shows a rather, broad, slightly rounded crown rim at the outer margins, with inner and outer parts joining in blunt mesial and distal angles. The crown-root junction lies in a relatively deep depression in the centre of the crown’s basal surface.

The high, narrow holaulacorhizid root is more or less oval in cross-section, slightly oblique toward the rear of the tooth, and slightly diverges at the root base. The root base presents a well-developed, deep and narrow median groove, with a relatively large aperture in the outer central base of the groove. Root coating is present at about one third of the upper part, all around the root.

Subfamily: Narkinace

The Narkidae comprise the genera Crassinarke, Heteronarce, Narke, Temera and Typhlonarke.

Genus: Crassinarke TAKAGI, 1951


This genus is monotypic with the type species C. dormitor.

Crassinarke dormitor TAKAGI, 1951

(Textplate 1; no SEM illustration of isolated teeth because the roots are too badly preserved)


HETERODONTY

The dentition is gradient monognathic heterodont with lateral and posterior teeth becoming lower and the cusp slightly inclined toward the commissure. Lacking a female and juvenile specimen sexual nor ontogenetic heterodonty could not be evaluated.

VASCULARIZATION

The teeth show the holaulacorhizid root type with an elongated, well developed pulp cavity, from which the vascular tubes of the circumpulpar dentine radiate into crown and root. Osteodentine and inner lateral foramina are absent. (See textfigure 5)
MALES AND FEMALES

The crown is divided by sharp mesial and distal cutting edges into an inner and outer face. The outer face shows a crown base that forms a blunt angle in the center, and overhangs the root. Both, mesial and distal cutting edges are of about equal size and curve upward to form a well-developed cusp; each joins the crown-base in a blunt angle. Lateral and posterior teeth become gradually lower and asymmetrical. The outer surface is slightly concave. Generally, the smooth inner face is concave, but the mid-section is convex. Inner and outer ornamentation are absent.

The basal surface of the crown shows a rather, broad, slightly rounded crown rim at the outer margins, with inner and outer parts joining in blunt mesial and distal angles. The crown-root junction lies in a relatively deep depression in the centre of the crown's basal surface.

The narrow holaulacorhizid root is more or less oval in cross-section, slightly oblique toward the rear of the tooth, and diverges at the root base. The root base presents a well-developed, deep and narrow median groove, with a relatively large aperture in the outer central base of the groove. Root coating is present at about one third of the upper part, all around the root. Inner and outer foramina are absent.

Genus: *Heteronarce* REGAN, 1921

New fishes from deep water off the coast of Natal. *Annals and Magazine of Natural History*, Series 9, 7 (41): 412-420. The genus comprises the species *H. bentuviai*, *H. garmani* (type species), *H. mollis* and *H. prabhiui*.

*Heteronarce garmani* REGAN, 1921
(Plate: 12; see also plate: 13)


HETERODONTY

The dentition is gradient monognathic heterodont with lateral and posterior teeth becoming lower and the cusp slightly inclining toward the commissure. Only a male specimen was at hand for this study, but female teeth were illustrated by CAPPETTA (1988), so that absence of sexual heterodonty could not be confirmed. Lacking juvenile material ontogenetic heterodonty could not evaluated.

VASCULARIZATION

The teeth the show holaulacorhizid root type with an elongated, well developed pulp cavity, from which the vascular tubes of the circumpulpar dentine radiate into crown and root. Osteodentine and inner lateral foramina are absent. (See textfigure 6)

MALES AND FEMALES

The crown is divided by sharp mesial and distal cutting edges into an inner and outer face. The outer face shows a slightly arched, rounded crown base, overhanging the root. Both, mesial and distal cutting edges are of about equal size and similarly arched, and continuously with the crown base. At about one third of the crown both cutting edges turn upward to form a cusp, half as high as the length of a cutting edge, that lowers gradually in lateral and posterior teeth. The outer surface is slightly concave. Generally, the smooth inner face is concave, but the mid-section is convex. Inner and outer ornamentation are absent.

The basal surface of the crown shows a rather, broad, slightly rounded crown rim at the outer margins, with inner and outer parts joining in blunt mesial and distal angles. The crown-root junction lies in a relatively deep depression in the centre of the crown's basal surface.

The moderately high, narrow holaulacorhizid root is more or less oval in cross-section, slightly oblique toward the rear of the tooth, and diverges at the root base. The root base presents a well-developed, deep and narrow median groove, with an aperture in the outer central base of the groove. Root coating is present at about one third of the upper part, all around the root.

Part of the dentition of a male of *Heteronarce mollis* is also illustrated on plate 13.

Genus: *Narke* KAUP, 1826

Beiträge zu Amphibiologie und Ichthyologie. Isis 19 (1): 87-90. The genus comprises the type species *N. capensis* and *N. dipterygia* and *N. japonica*. Lacking tooth material of the type species *N. dipterygia* was used instead for description and illustration.

*Narke dipterygia* (BLOCH & SCHNEIDER, 1801)
(Plate: 14 )

Torpedo *dipterygia* BLOCH & SCHNEIDER 1801 M.E. BLOCHII Systema Ichtyologiae iconibus ex illustratum. Post

HETERODONTY

The dentition is gradient monognathic heterodont with lateral and posterior teeth becoming lower and the cusp slightly inclining toward the commissure. Only a female specimen was at hand for this study, but male teeth were illustrated by CAPPETTA (1988), so that the absence of sexual heterodonty could not be confirmed. Ontogenetic heterodonty is presented by less developed, lower cusps in juveniles.

VASCULARIZATION

The teeth show the holaulacorhizid root type with an elongated, well-developed pulp cavity, from which the vascular tubes of the circumpulpar dentine radiate into crown and root. Osteodentine and inner lateral foramina are absent. (See textfigure 7)

MALES AND FEMALES

The crown is divided by sharp mesial and distal cutting edges into an inner and outer face. The outer face shows an arched, rounded crown base with an apron-like bulge, overhanging the root. Both, mesial and distal cutting edges are somewhat irregularly straight, more or less of equal size; each joins the crown base in a blunt angle, and both merge in an apex, giving the outer face a triangular appearance, that slightly lowers gradually in lateral and posterior teeth. The outer surface is slightly concave. Generally, the smooth inner face is concave, but the mid-section is convex. Inner and outer ornamentation are absent.

The basal surface of the crown shows a rather, broad, slightly rounded crown rim at the outer margins, with inner and outer parts joining in blunt mesial and distal angles. The crown-root junction lies in a relatively deep depression in the centre of the crown’s basal surface.

The moderately high, narrow holaulacorhizid root is more or less oval in cross-section, slightly oblique toward the rear of the tooth, and diverges at the root base. The root base presents a well-developed, deep median groove, with an aperture in the outer central base of the groove. Root coating is present at about one third of the upper part, all around the root.

Genus: Temera GRAY, 1836

Description of twelve new genera of fish, discovered by General Hardwicke in India, the greater part in the British Museum. Zoological Miscellany 1: 4-9.

The genus is monotypic with the type species T. hardwicki.

Temera hardwicki GRAY, 1836

(Plate : 15)

Temera hardwicki GRAY, 1836 Description of twelve new genera of fish, discovered by General Hardwicke in India, the greater part in the British Museum. Zoological Miscellany 1: 4-9.

HETERODONTY

The dentition is gradient monognathic heterodont, with lateral and posterior teeth lowering toward the commissure. Lacking material of juveniles and full-grown females, ontogenetic or sexual heterodonty could not be determined. However, the low crown with a transverse keel instead of a cusp indicates absence of sexual heterodonty.

VASCULARIZATION

The teeth show an adapted, holaulacorhizid root type with a relatively small pulp cavity. The vascular tubes of the circumpulpar dentine radiate into crown and root. Osteodentine and inner lateral foramina are absent. (See textfigure 8)

MALES AND FEMALES

In occlusal view, the crown is mesio-distally broad and exhibits an inward bent, relatively high transverse keel, which is often flattened by abrasion, and lowers gradually in lateral and posterior teeth. It divides the crown into an inner and outer part. The outer and inner margins of the crown are more or less equally arched, and both margins join in sharp mesial and distal angles. The smooth inner face is concave with a weak bulging of the upper central part. The outer face’s upper part is concave, changing into an apron-like lower part, that is strongly convex and sometimes presenting a central depression. Inner and outer ornamentation are absent. The basal surface of the crown shows a broad, slightly convex crown rim at the outer margin, gradually narrowing to half its width at the inner part. The crown-root junction lies in a shallow depression in the centre of the crown’s basal surface. The high, narrow holaulacorhizid root is more or less oval in cross-section, slightly oblique toward the rear of the tooth, and diverges at the root base. The root base presents a well-
developed, median groove, with an aperture in the outer central base of the groove. Root coating is present at about one third of the upper part, all around the root.

Genus: *Typhlonarke* WAITE, 1909

Scientific results of the New Zealand government trawling expedition 1907. Records of the Canterbury Museum 1: 41-156. The genus comprises the type species *T. aysoni* and *T. tarakea*.

**Typhlonarke aysoni** (HAMILTON, 1902)  
(Plates 17 and 18)

*Astrape aysoni* HAMILTON, 1902 Notice of an electric ray new to the fauna of New Zealand, belonging to the genus *Astrape*. Transactions and Proceedings of the New Zealand Institute 34: 224-226

HETERODONTY

The dentition is gradient monognathic heterodont with lateral and posterior teeth becoming lower and the cusp slightly inclined toward the commissure. Only a male specimen was at hand for this study, but a female was illustrated by CAPPETTA (1988), so that absence of sexual heterodonty is confirmed. Lacking juvenile material ontogenetic heterodonty could not be examined.

VASCULARIZATION

The teeth show the holaulacorhizid root type with an elongated, well developed pulp cavity, from which the vascular tubes of the circumpulpar dentine radiate into crown and root. Osteodentine and inner lateral foramina are absent. (See textfigure 9)

**MALES AND FEMALES**

The crown is divided by sharp mesial and distal cutting edges into an inner and outer face. The outer face shows an arched, rounded crown base with an apron-like bulging, overhanging the root. Both, mesial and distal cutting edges are of about equal size and blade-like, each joining with the crown base in a blunt angle. At about one third of the crown both cutting edges turn upward to form a cusp, half as or equally as high as the length of a cutting edge and lowering gradually in lateral and posterior teeth. The outer surface is slightly concave. Generally, the smooth inner face is concave, but the midsection is slightly convex. Inner and outer ornamentation is absent. The basal surface of the crown shows a rather, broad, slightly rounded crown rim at the outer margins, with inner and outer parts joining in blunt mesial and distal angles. The crown-root junction lies in a relatively deep depression in the center of the crown's basal surface. The generally small, narrow holaulacorhizid root is more or less oval in cross-section, slightly oblique toward the rear of the tooth, and diverges at the root base. The root base presents a well-developed, narrow median groove, with an aperture in the outer central base of the groove. Root coating is present at about one third of the upper part, all around the root.

Family: Torpedinidae  
Subfamily: Hypninae  
Genus: *Hypnos* DUMERIL, 1852

Monographie de la famille des Torpédiniens, ou poissons plagiostomes électriques, comprenant la description d'un genre nouveau, de trois espèces nouvelles, et de deux espèces nommées dans le Musée de Paris, mais non encore décrites. Rev. Magazine de Zoologie (ser.2) 4: 176-189. The genus comprises the type species: *H. monopterygium* and *H. submigrum*.

**Hypnos monopterygium** SHAW & NODDER, 1794  
(Plates: 19 and 20)


HETERODONTY

The dentition is gradient monognathic heterodont with lateral and posterior teeth becoming lower and the cusp slightly inclined toward the commissure. Sexual and ontogenetic heterodonty are absent.

VASCULARIZATION

The teeth show the holaulacorhizid root type with an elongated, well developed pulp cavity, from which the vascular tubes of the circumpulpar dentine radiate into crown and root. Osteodentine and inner lateral foramina are absent. (See textfigure 10)

**MALES AND FEMALES**

The tri-cuspid crown is structured by sharp mesial and distal cutting edges at each side of the cusps dividing the crown into an inner and outer face. The outer face shows an almost straight to slightly arched crown base, overhanging the root. The extremely elongated cusps are constricted at their base, and the central one can be more than seven times as high as...
its base width, the mesial and distal cusps can be up to five times as high as their base width. The latter ones slightly curve away from the central cusp. The three cusps are positioned next to each other, in occlusal view, the central one stands slightly backwards and is slightly more bent inward. The teeth only diminish in their general size and the three cusps only slightly become more oblique distally in lateral and posterior teeth. The outer surface is slightly concave. Generally, the inner face of the cusps is strongly convex and from the cusps, the inner face protrudes almost horizontally inward to a central basal depression at the inner margin. Inner and outer ornamentation is absent.

The basal surface of the crown has a rather, broad, slightly rounded crown rim at the outer margins, and is more or less quadrangular with blunt mesial and distal angles. The crown-root junction lies in a relatively narrow depression in the centre of the basal crown’s surface.

The low, broad holaulacorhizid root is slightly oblique toward the rear of the tooth, and diverges at the root base. The root base presents a well-developed, deep and very broad median groove, with an aperture in the outer central base of the groove and sometimes one or several scattered smaller apertures. Root coating is present at about one third of the upper part, all around the root.

Subfamily: Torpedininae
Genus: Torpedo HOUTTUYN, 1764

Natuurlyke historie of uitvoerige beschrywing der dieren, planten en mineraalen, volgens het samenstel van den Heer Linnaeus Met nauwkeurige afbeeldingen. 3 vols. in 37 parts.

The genus was subdivided by Gill (1862) into the two subgenera T.(Torpedo) and T.(Tetronarke). The former comprises the species T. andersoni, T. alexandrianus, T. bauchotae, T. fuscomaculata, T. marmorata, T. mackayana, T. panthera, T. sinuspressici, T. panthera, T. torpedo (type species), and another new species from the Gulf of Aden (CARVALHO, M., STEHMANN, M.F.W., MANILO, L.G. in press. T.(Tetronarke) comprises the species T. california, T. fairchildi, T. microdiscus, T. nobiliana (type species), T. puelcha, T. semipelagica, T. tokionis and T. tremens.

Subgenus: Torpedo (Tetronarke) GILL, 1862


Torpedo (Tetronarke) nobiliana BONAPARTE, 1835 (Plates: 21 and 22)


HETERODONTY

The dentition is gradient monognathic heterodont with lateral and posterior teeth becoming lower and the cusp inclined toward the commissure. Sexual and ontogenetic heterodonty are absent.

VASCULARIZATION

The teeth show the holaulacorhizid root type with an elongated, well developed pulp cavity, from which the vascular tubes of the circumpulpar dentine radiate into crown and root. Osteodentine and inner lateral foramina are absent. (See textfigure 11)

MALES AND FEMALES

The crown is divided by sharp mesial and distal cutting edges into an inner and outer face. The outer face shows an upward arched, rounded crown base, overhanging the root. Both, mesial and distal cutting edges are of about equal size, each joining seamlessly with the crown base. They curve abruptly upward to form a broad-based, elongated cusp and joint apex, more than ones as high as the length of each cutting edge. The cusp becomes lower gradually in lateral and posterior teeth. The outer surface is slightly concave, with a basal central depression, giving the impression of mesial and distal basal lobes. Generally, the smooth inner face is concave, but the mid-section is convex, the mesial and distal lower lobe-like parts protruding inwardly. Inner and outer ornamentation are absent.

The basal surface of the crown has a rather, broad, slightly rounded crown rim at the outer margins, and is more or less quadrangular with blunt mesial and distal angles. The crown-root junction lies in a relatively narrow depression in the centre of the basal crown’s surface.

The low, broad holaulacorhizid root is slightly oblique toward the rear of the tooth, and diverges at the root base. The root base presents a well-developed, deep and very broad median groove, with an aperture in the outer central base of the root.
Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites

the groove and sometimes one or several scattered smaller apertures. Root coating is present at about one third of the upper part, all around the root.

Subgenus: *Torpedo (Torpedo) HOUTTUYN, 1764*

*Natuurlyke historie of uitvoerige beschrywing der dieren, planten en mineraalen, volgens het samenschil van den Heer Linnaeus. Met nauwkeurige afbeeldingen. 3 vols. in 37 parts. Natuurlyke historie, Amsterdam 1761-1785*

*Torpedo (Torpedo) torpedo LINNAEUS, 1758* (Plates: 23 to 26)


**HETERODONTY**

The dentition is gradient monognathic heterodont with lateral and posterior teeth becoming lower and the cusp inclined toward the commissure. Sexual and ontogenetic heterodonty are absent.

**VASCULARIZATION**

The teeth show the holaulacorhizid root type with an elongated, well developed pulp cavity, from which the vascular tubes of the circumpulpar dentine radiate into crown and root. Osteodentine and inner lateral foramina are absent. (See textfigure 12)

**MALES AND FEMALES**

The crown is divided by sharp mesial and distal cutting edges into an inner and outer face. The outer face shows a rounded, upward arched crown base, overhanging the root. Both, mesial and distal cutting edges are of about equal size and continuous with the crown base. They curve from abruptly upward to form a broad-based, elongated cusp and joint apex being twice or more as high as the length of each cutting edge. The cusp becomes lower gradually in lateral and posterior teeth. The outer surface is slightly concave, with a basal central depression, which gives the impression of mesial and distal basal lobes. Generally, the smooth inner face is concave, but the mid-section is convex, with the mesial and distal lower lobe-like parts protruding inward. Inner and outer ornamentation are absent.

The basal surface of the crown has a rather, broad, slightly rounded crown rim at the outer margins, and is more or less quadrangular with blunt mesial and distal angles. The crown-root junction lies in a relatively narrow depression in the centre of the basal crown's surface. The low, broad holaulacorhizid root is slightly oblique toward the rear of the tooth, and diverges at the root base. The root base presents a well-developed, deep and very broad median groove, with an aperture in the outer central base of the groove and sometimes one or several scattered smaller apertures. Root coating is present at about one third of the upper part, all around the root.

Family: not defined

Genus: *Bengalichthys ANNANDALE, 1909*


The genus is monotypic with the type species *B. impennis*.

*Bengalichthys impennis ANNANDALE, 1909* (Plate: 16)


**HETERODONTY**

The dentition is gradient monognathic heterodont, with lateral and posterior teeth lowering toward the commissure. Lacking material of juveniles and full-grown females, ontogenetic and sexual heterodonty could not be determined.

**VASCULARIZATION**

The teeth show an adapted, holaulacorhizid root type with a relatively small pulp cavity. The vascular tubes of the circumpulpar dentine radiate into crown and root. Osteodentine and inner lateral foramina are absent. (See textfigure 13)

**MALES AND FEMALES**

The crown is divided by sharp mesial and distal cutting edges into an inner and outer face. The outer face shows an arched, rounded crown base overhanging the root. Both, mesial and distal cutting edges are straight, more or less of equal size, and joining the crown base in an angle. Both cutting edges join in an apex, giving the outer face a triangular appearance,
which lowers gradually in lateral and posterior teeth. The outer surface is slightly concave. Generally, also the smooth inner face is concave. Inner and outer ornamentation are absent.

The basal surface of the crown shows a rather broad, slightly rounded crown rim at the outer margins, with inner and outer parts joining in mesial and distal angles. The crown-root junction lies in a relatively deep depression in the centre of the basal crown’s surface.

The moderately high, narrow holaulacorhizid root is more or less oval in cross-section, slightly oblique toward the rear of the tooth, and diverges at the root base. The root base presents a well-developed median groove, with a large aperture in the outer central base of the groove. Root coating is present at about one third of the upper part, all around the root.

**Differential diagnosis**

The most significant tooth morphology characters are summarized in table 1. Generally for Torpediniformes, the most characteristic part is the outer face of the crown, particularly the absence or presence of a cusp, its shape and the shape of the mesial and distal cutting edges. Further, the type of root is significant: a narrow and high or moderately high or low and broad root. *Hypnos, T(Tetronarke)* and *T(Torpedo)* share a low and broad root. The tricuspid crown is typical for *Hypnos*. There are minor odontological differences between *T(Tetronarke)* and *T(Torpedo)* only, which may only be interspecific variation.

Among the remaining taxa with a high to moderately high, narrow root, only *Temera* possesses a transverse keel. *Bengalichthys, Crassinarke* and *Narke* share a more or less triangularly shaped crown. The cutting edges of *Bengalichthys* are straight, those of *Crassinarke* slightly curved upward and those of *Narke* irregularly, more or less undulated. *Benthobatis, Diplobatis, Discopyge, Heteronarce, Narcine* and *Typhlonarke* all possess a central cusp, which is more or less resulting from the shape of the mesial and distal cutting edges. With the exception of *Benthobatis* and *Heteronarce*, with upward curving cutting edges, cutting edges of the remaining taxa are more or less blade-like. The cusp of *Benthobatis* is narrow, whereas that of *Heteronarce* is broader and more massive. The cutting edges of *Benthobatis* are irregularly shaped, but smooth in *Heteronarce*. The mesial and distal blades of *Diplobatis, Discopyge* and *Narke* join the cusp base in a notch. Those of *Typhlonarke* are continuous with the cusp base. The notches of *Diplobatis* are shallow and the cusp is low, whereas in *Discopyge* and *Narke*, the notches are deeper and the cusp is high to moderately high. Generally, the cusps of *Discopyge* are lower than those of *Narke*. However, the tooth morphology differences between *Diplobatis, Discopyge* and *Narke* are minor and may vary within these taxa.

**Conclusions**

From the odontological point of view the Torpediniformes can be divided into two major groups by their typical root type. *Hypnos, T(Tetronarke)* and *T(Torpedo)* have a low broad root. All remaining taxa possess a narrow and high or moderately high root.

Group 1

*Hypnos* and *Torpedo* are considered as separate evolutionary developments. The odontological differences between *T(Tetronarke)* and *T(Torpedo)* are minimal and do not support retaining two separate subgenera.

**Table 1. General morphologically significant characters**

<table>
<thead>
<tr>
<th>Species</th>
<th>Crown</th>
<th>Root</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bengalichthys</td>
<td>Cusp triangular Cutting edges straight</td>
<td>Moderately high and narrow</td>
</tr>
<tr>
<td>Benthobatis</td>
<td>Cusp narrow and moderately high Cutting edges curved upward</td>
<td>Moderately high and narrow</td>
</tr>
<tr>
<td>Diplobatis</td>
<td>Cusp narrow and moderately high Cutting edges blade-like</td>
<td>Moderately high and narrow</td>
</tr>
<tr>
<td>Discopyge</td>
<td>Cusp narrow and high Cutting edges blade-like</td>
<td>Moderately high and narrow</td>
</tr>
<tr>
<td>Crassinarke</td>
<td>Cusp triangularly Cutting edges slightly curved upward</td>
<td>Moderately high and narrow</td>
</tr>
<tr>
<td>Heteronarce</td>
<td>Cusp relatively broad Cutting edges curving upward</td>
<td>Moderately high and narrow</td>
</tr>
<tr>
<td>Narcine</td>
<td>Cusp narrow and high Cutting edges blade-like</td>
<td>Moderately high and narrow</td>
</tr>
<tr>
<td>Narke</td>
<td>Cusp triangular Cutting edges straight</td>
<td>Moderately high and narrow</td>
</tr>
<tr>
<td>Temera</td>
<td>Transversal keel high</td>
<td>Low and narrow</td>
</tr>
<tr>
<td>Typhlonarke</td>
<td>Cusp relatively broad Cutting edges blade-like, curving upward</td>
<td>Low and broad</td>
</tr>
<tr>
<td>Hypnos</td>
<td>Tricuspid</td>
<td>Low and broad</td>
</tr>
<tr>
<td>Torpedo (Tetronarke)</td>
<td>Cuts high Cutting edges blade-like, curving upward</td>
<td>Low and broad</td>
</tr>
<tr>
<td>Torpedo (Torpedo)</td>
<td>Cuts high Cutting edges blade-like, curving upward</td>
<td>Low and broad</td>
</tr>
</tbody>
</table>
Contributions to the study of the comparative morphology of teeth and other relevant ichthyodoruhtes

Group 1
Root low and broad

Crown unicuspid
Torpedo

Hypnos

Crown tricuspid

Cutting edges curved upward
Benthobatis
Heteronarce

Cutting edges blade-like
Diplobatis
Discopyge
Narcine
Typhlonarke

Group 2
Root high and narrow

Cusp triangular

Bengalichthys
Crassinarke
Narke

Transverse keel
Temera

Group 2
This group is subdivided into three separate evolutionary lines:
Subgroup 1 Temera with a transverse keel and more or less dasyatid appearance.
Subgroup 2 Bengalichthys, Crassinarke and Narke with their more or less triangularly shaped crown.
Subgroup 3 Benthobatis, Diplobatis, Discopyge, Heteronarce, Narcine and Typhlonarke with their particular cusp and mesial and distal cutting edges.

Within this subgroup Benthobatis and Heteronarce are different by the shape of mesial and distal cutting edges, as well as Diplobatis, Discopyge, Narcine and Typhlonarke are characterized by the shape of mesial and distal blades and cusp. Probably due to the small size of the torpediniform microteeth, there are only few fossil records known. However, their tooth morphology shows similarity with the dasyatids, which particularly is documented in Temera. Not only the transversal keel, but the whole tooth morphology has similarity with dasyatids, and the Torpediniformes may well have derived from the Dasyatidae.

The lack of sexual heteronty appears to be a more advanced stage of development.
The vascularization of the teeth of all torpediniform taxa is principally the same. The orthodont type, lacking osteodentine in the root, is also an indication of an advanced development.

Acknowledgements
The authors thank Prof. Dr. H. Wilkens, Zoologisches Institut und Zoologisches Museum der Universität Hamburg (ZMH), Dr. H. Ishihara, Museum of the Tokyo University of Fisheries (MTUF), Mr. B. Seret, Antenne XXX, Musée National d’Histoire Naturtelle, Paris (NMHN), Dr. D. Nolf, Institut Royal des Sciences naturelles de Belgique, Brussels (IRSNB) and Mr. C. Hartman, Ryan’s Falls (Australia) for permission to examine specimens at their disposal. The SEM-photographs were taken by J. Cillis, Institut Royal des Sciences naturelles de Belgique, Brussels.

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**General glossary**  
(applying to all previous issues of this series)

**Concerning the jaw**

Anterior  
Tooth position close to junction of left and right jaw halves.

Commissural  
Tooth position near the end of jaw.

Dignathic  
Heterodont by having different tooth morphology in upper and lower jaws.

File  
Tooth row from symphysis toward end of jaw.

Heterodonty  
Different tooth morphology within a tooth file. There are two types of heterodonty: dignathic and monognathic.

Homodonty  
Uniform tooth morphology within a tooth file.

Lateral  
Tooth positions half way along the jaw.

Longitudinal  
Symphysial/commissural direction of a tooth file.

Monognathic  
Heterodonty within one jaw only. (this can appear as gradient or disjunct)

Parasympathial  
First anterior tooth row, if a symphysial tooth row is absent.

Posterior  
Tooth positions toward the angle of jaws.

Pseudosymphial  
One of the parasympathial tooth rows placed in the position of the symphysial tooth row (symmetry).

Row  
Tooth row from inner face to outer face of jaw.

Symphysial  
Teeth at junction of both halves of a jaw.

Transverse  
Outer/inner direction of a row.

**Concerning the tooth**

An-, Hemi-, Hol- and Polyaulacorhizid  
Concerning their vascularization. E. Castier (1947) recognized and described four phylogenetically significant root types within the orthodont histotypes of elasmobranch teeth.

Anaulacorhizid  
Vascularization through scattered foramina of equal size on both outer and inner faces, (e.g. Hexanchidae).

Hemiaulacorhizid  
Vascularization through a median groove and 1 or 2 lateral foramina on inner face, (like in Squatinidae and Orectolobidae)

Holaulacorhizid  
Vascularization through many small foramina concentrated in a median groove running from outer to inner face, (e.g. Rajidae)

Polyaulacorhizid  
Vascularization through many small foramina concentrated in several grooves running parallel from outer to inner face. (e.g. Myliobatidae)

Apron  
Expansion of the central part of the outer crown base.

Basal  
Bottom face concerned.

Inner central ridge  
Convex protrusion at the upper midsection of the inner crown face.

Costules  
Short, vertical ridges sometimes present on inner and/or outer crown base.

Crown  
Enamelated tooth part.

Distal  
Tooth edge or part toward angle of jaws.

Histotype  
Type of internal tooth vascularization.

Inner face  
Viewed from inside the mouth.

Longitudinally  
Apico-basally directed structuring on a tooth.

Median groove  
Groove running from the inner root base to the inner crown-root junction, dividing a holaulacorhizid type of root into two root lobes. It includes the main foramina of the vascularization system.
Mesial
Tooth edge or part toward junction (symphysis) of left and right jaw halves.

Neo-holaulacorhizid
Modification of the holaulacorhizid type of root, combining a shallow median groove and an extremely expanded pulp cavity.

Orthodont
Histotype of vascularization, by which a tooth is supplied primarily by an internal pulp cavity radiating into numerous tiny canals penetrating the orthodentine layer.

Osteodont
Histotype of vascularization, by which a tooth is supplied without any pulp cavity by scattered tiny cavities and canals penetrating the osteodentine layer of the root and the internal crown material.

Outer face
Viewed from outside the mouth.

Pseudo-apron
Apron-like vertical ridges that appear sometimes on lateral and posterior teeth.

Pseudo-osteodont
The former pulp cavity of an originally orthodont histotype of tooth being filled secondarily with osteodentine.

Pulp cavity
Cavity inside the tooth from which the vascularization is spread via canaliculi.

Root
Non-enamelated tooth part, that forms the junction with the jaw gum and provides vascularization of the tooth.

Root coating
Coating on the upper part of the root (probably enamelioid)

Root stem
Root part between the crown base and root lobe section.

Secondary anaulacorhizid
Median groove of a holaulacorhizid type of root totally overgrown to form a closed tube internally connected or merged with the pulp cavity

Secondary hemialulacorhizid
Median groove of holaulacorhizid type of root overgrown to various extent, converting the median groove to an internal tube, which is merged with the pulp cavity.

Striae
Vertical ridges running from crown base toward apex.

Sulcus
Groove developed by the primary vascularization canals leading from root base to the main foramina in anaulacorhizid root type. It differs from the median groove in which several foramina are concentrated of the holaulacorhizid root type and the parallel grooves of the polyaulacorhizid root type, respectively, in that a sulcus lacks foramina.

Transverse
Mesio-distally directed.

Transverse keel
Transverse ridge dividing the crown into inner and outer face.

Uvula
Lobate extension of the inner crown base.

Composition of the plates
As far as possible plates of isolated teeth of one juvenile (male or female) and of both male and female adults are presented for each supraspecific taxon.
The plates have a consistent composition: upper teeth are presented with their cusps downward and lower teeth with their cusps upward.
The choice of left or right jaw halves illustrated depends on the preservation quality of the specimen's tooth files only.

Legend

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
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</thead>
<tbody>
<tr>
<td>a</td>
<td>anterior position</td>
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<tr>
<td>la</td>
<td>latero-anterior</td>
</tr>
<tr>
<td>l</td>
<td>lateral position</td>
</tr>
<tr>
<td>lp</td>
<td>latero-posterior</td>
</tr>
<tr>
<td>p</td>
<td>posterior position</td>
</tr>
<tr>
<td>c</td>
<td>commissural position</td>
</tr>
</tbody>
</table>
Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites

Plate 2. *Bacillithoreus maculatus* Bean & Weed, 1909. Female 38.5 cm TL, off Florida. Upper and lower teeth.
Plate 3. *Diplobatis ommata* (JORDAN & BOLLMAN, 1890). Female 15 cm t.l., off Panama. Upper teeth.
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Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites

Plate 11. Nanurus brasiliensis (Olsers, 1831), Male 49 em L, off Brazil. Upper and lower teeth.
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Plate 14. *Nerke depocyra* (BLOCH & SCHNEIDER, 1801), Female 18 cm l.t., off Puri, India. Upper and lower teeth.
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Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites
Plate 25. *Torpedo (Torpedo) torpedo* (Linnæus, 1758). Male 41 cm t.L. off Dakar, Senegal. Upper teeth. Central lower part of the plate, radicular view of an uncommon example of the fusion of two dental germinae of commissural teeth.
Plate 26. *Torpedo (Torpedo) torpedo* (Linnaeus, 1758). Male 41 cm t.l., off Dakar, Senegal. Lower teeth. Central upper part of the plate, outer view of an uncommon example of the fusion of two dental germinae of commissural teeth.