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Results of the research cruises of FRV "Walther Herwig" to South America. XXXVIII.[1]) Osteology and Relationships of the Ceratioid Anglerfish Genus *Spiniphryne* (Family Oneirodidae).

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With 6 figures and 1 table

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Kurzfassung

Ergebnisse der Forschungsreisen des FFS „Walther Herwig" nach Südamerika. XXXVIII. Osteologie und Verwandtschaftsbeziehungen der Tiefsee-Angler-Gattung *Spiniphryne* (Family Oneirodidae).

Die Anglerfisch-Gattung *Spiniphryne* wird auf der Grundlage neuen Materials diagnostiziert und osteologisch beschrieben. Die der Arbeit zugrunde liegenden drei Exemplare wurden im tropischen Ostatlantik gefangen; sie sind die einzigen außer dem von Bermuda stammenden Holotypus bekannten Vertreter der Gattung. Obwohl ursprünglich mit der oberflächlich ähnlichen Gattung *Centrophryne*, Familie Centrophrynidae, assoziiert, scheint doch die Gattung *Oneirodes*, Familie Oneirodidae, der nächste Verwandte von *Spiniphryne* zu sein. Auf Grund weitreichender Ähnlichkeit und gemeinsamer abgeleiteter Merkmale muß *Spiniphryne* als ursprünglichster Oneirodide gelten, der dem anzestralen Bestand, aus welchem die Familie Oneirodidae hervorging, sehr ähnlich ist.

Abstract

The ceratioid anglerfish genus *Spiniphryne* is diagnosed and described osteologically on the basis of new material recently collected from the eastern tropical Atlantic Ocean. Although, previously associated with the superficially similar genus *Centrophryne*, family Centrophrynidae, the closest relative of *Spiniphryne* appears to be *Oneirodes* of the family Oneirodidae. On the basis of overall similarity and shared derived character states, *Spiniphryne* is the least derived oneirodid, most like the ancestral stock which gave rise to the family Oneirodidae.

A. Introduction

The taxonomic history of the genus *Spiniphryne* begins with Beebe's (1932) description of *Dolopichthys gladisfenae*, based on a single female specimen, 40.0 mm standard length, collected from off Bermuda. Six months after Beebe's (1932) publication, Regan and Trewavas (1932) introduced *Centrophryne*, a new genus of the family Oneirodidae, to include *D. gladisfenae* and a new species which they named *C. spinulosa*. The presence

[1]) Ergebnisse der Forschungsreisen des FFS „Walther Herwig" nach Südamerika. XXXVII. Untersuchungen zur inneren hydrographischen Struktur des südlichen und mittleren Atlantiks (0-2000 m Tiefe) mit zoogeographischen Anmerkungen. Von Walter Lenz in Ber. dt. wiss. Kommn. Meeresforsch. 24 (1): 1—22, 1975.

in *C. spinulosa* of four pectoral radials, an anteriorly directed spine on the subopercular bone, and a small, digitiform hyoid barbel led BERTELSEN (1951) to remove this species from the Oneirodidae and place it in a new family, the Centrophrynidae. *Centrophryne gladisfenae* was retained by BERTELSEN (1951) within the family Oneirodidae under a new generic designation, *Spiniphryne (Bertelsenna* of WHITLEY, 1954, an unacceptable replacement name for *Spiniphryne)*. In a review of the family Centrophrynidae, PIETSCH (1972) retained *Spiniphryne* within the Oneirodidae following BERTELSEN (1951) but predicted that sufficient material of *S. gladisfenae* would show this species and *C. spinulosa* to be congeneric. For this reason, and because specimens of the genus were heretofore unavailable, PIETSCH (1974) did not include *Spiniphryne* in an osteological study of oneirodid genera.

An osteological examination of *Spiniphryne* made possible by the collection of two female specimens during the 1971 cruise of the "Walther Herwig" to the south Atlantic, has shown that, although superficially quite similar to *Centrophryne*, the closest relatives of *Spiniphryne* are among the least derived members of the family Oneirodidae.

B. Methods and Materials

All fish lengths are standard lengths (SL). All measurements were taken on the left side whenever possible and rounded to the nearest 0.1 mm. To insure accurate fin-ray counts, skin was removed from the pectoral fins and incisions made to reveal the rays of the dorsal and anal fins. Sockets, indicating missing teeth in the jaw and on the vomer, were included in total tooth counts. Jaw tooth counts are the sum of both right and left sides. Head length is the distance from the anterior tip of the upper jaw to the posteriormost margin of the preoperculum. Head width is the distance between the tips of the sphenotic spines. Head depth is the distance from the tip of the sphenotic spine to the base of the quadrate spine. Lower jaw length is the distance from the symphysial spine to the posteriormost margin of the articular. Illicium length is the distance from the articulation of the pterygiophore of the illicium and the illicial bone to the dorsal surface of the escal bulb, excluding escal appendages. Terminology used in describing the various parts of the angling apparatus follows BRADBURY (1967). Definitions of terms used for the different stages of development follow BERTELSEN (1951).

This study is based on three metamorphosed female specimens ranging in size from 12.8 to 63.0 mm. One of these, a 49.0 mm specimen, was cleared in KOH and stained with alizarin red S and forms the basis for the following osteological description. Where possible, dissections were made of uncleared specimens to confirm observations made on the cleared specimen and to determine ontogenetic change. A complete osteological description is not given as most elements of the skeleton do not differ substantially from those of ceratioids previously described; only those aspects that show significant morphological similarity or difference from known ceratioids appear below. The material is deposited in the Institut für Seefischerei, Hamburg (ISH) and at the Institute of Oceanographic Sciences, Surrey (IOS; formerly the National Institute of Oceanography).

C. Osteology

a) *Cranium* (Figs. I, A—C)

The ethmoid cartilage and underlying vomer are slightly wider than the distance between the anterolateral tips of the frontals. An anterolateral keel of the ethmoid

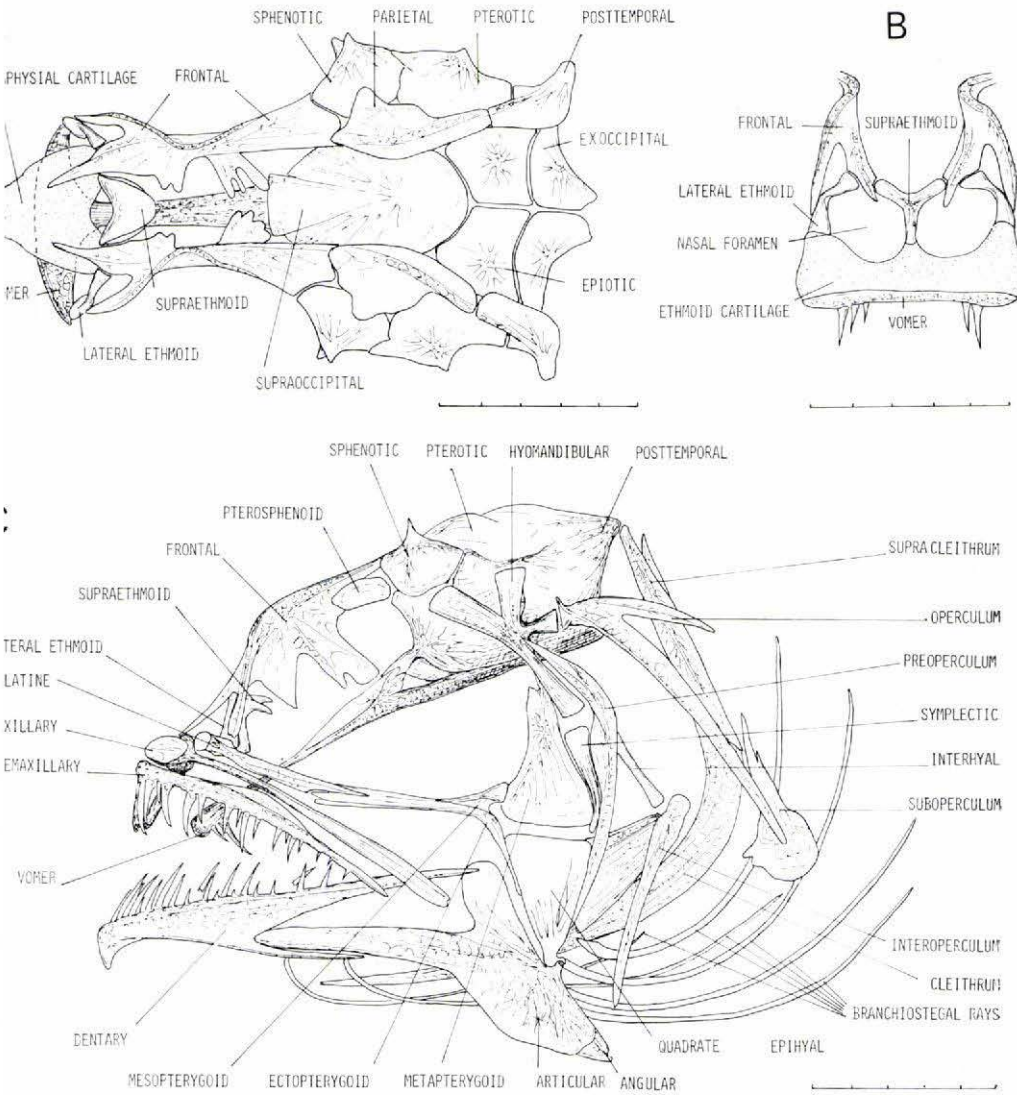

Fig. 1: A) Dorsal view of cranium of *Spiniphryne gladisfenae* with symphysial cartilage of upper jaw in place. B) Anterior view of anterior half of cranium of *Spiniphryne gladisfenae*. C) Lateral view of skull of *Spiniphryne gladisfenae* with part of pectoral girdle and hyoid apparatus in place.

cartilage is absent (present in *Centrophryne*; see PIETSCH, 1972: 27, Figs. 7—10). The ventromedial process of the supraethmoid, together with the lateral ethmoids and concave, dorsal surface of the ethmoid cartilage, form large, nearly circular nasal foramina. The lateral ethmoids are large, contributing nearly one fourth of the perimeter of the nasal foramina. The ventral surface of the vomer may bear up to three recurved and depressible teeth arranged in a transverse row on each side.

The dorsally convex frontals are shorter than the distance between the anterolateral tips of the sphenotics, and lie posterior to the ethmoid region. Ventromedial extensions of the frontals approach each other on the midline. There is no connection between the frontal and prootic. The space formed by the supraethmoid, the ventromedial margins of the frontals, the prootics, and the parasphenoid is free of cartilage, except for a narrow, dorsally-directed, posteromedial extension of the ethmoid cartilage which meets with ventromedial extensions of the frontals, and the posterior margin of the supraethmoid. The dorsomedial margins of the frontals and the thin, weakly ossified parietals diverge posteriorly, the posterior end of the illicial trough being considerably wider and shallower than its anterior end (among oneirodids, found only in *Oneirodes* and *Pentherichthys*; PIETSCH, 1974: 19). A well-developed, semi-circular pterosphenoid is present lying ventral to the posterior end of each frontal.

Each sphenotic is a dorsolaterally directed, cone-shaped element, the apex of which forms a well-developed spine. Posterolaterally, the sphenotic is overlapped by an anterodorsal process of the respective pterotic.

b) *Mandibular, Palatine and Hyoid Arches* (Fig. 1 A—C; Fig. 2 B)

The anterior tips of the premaxillaries are attached to each other by fibrous connective tissue and by a broad ligament which passes ventral to the anterior end of a large, roughly triangular, symphysial cartilage. The symphysial cartilage is longer than wide and posteriorly notched, the posterior lobes fitting into the large nasal foramina formed by the supraethmoid, ethmoid cartilage, and lateral ethmoids. On each side, the posterior ends of the premaxillary and maxillary bones are united by a strong ligament that passes anteriorly to attach to the labial cartilage of the dentary (PIETSCH, 1972: 31). The elongate portion of each premaxillary may bear as many as 21 recurved, depressible teeth.

Anteriorly, the dentaries meet on the midline forming a strong symphysial spine. The labial cartilage is well-developed. Each dentary may bear up to 24 recurved, depressible teeth. At its articulation with the quadrate, the articular forms a small, posterolaterally directed spine which is connected by a ligament to the ventral tip of the preoperculum.

Anteriorly, the upper half of each metapterygoid forms a thin, weakly ossified flange, the concave dorsal margin of which is attached to the anterodorsal margin of the hyomandibular by a sheet of connective tissue (previously known only in *Oneirodes*; PIETSCH, 1974: 9, Fig. 8). Dorsally, the hyomandibular forms a double head that articulates anteriorly in an area bordered by the sphenotic, prootic, and pterotic, and posteriorly on the ventrolateral face of the pterotic. At its articulation with the articular, the quadrate forms a rudimentary spine that is connected by a small ligament to an equally small mandibular spine.

There are two well-ossified hypohyals on each side. The six branchiostegal rays are cylindrical in cross-section for most of their length and are not compressed as in *Centrophryne* (PIETSCH, 1972: 34, Figs. 12, 14).

c) *Opercular Apparatus* (Fig. 1 C; Fig. 2 A)

The posterior margin of each operculum is deeply notched the two forks of which form an angle of approximately 38°. The length of the upper fork is 46.7 percent of the length of the lower fork. The suboperculum is elongate in the 49.0 mm specimen, the upper end tapering to a point; the lower end is circular without an anterior spine

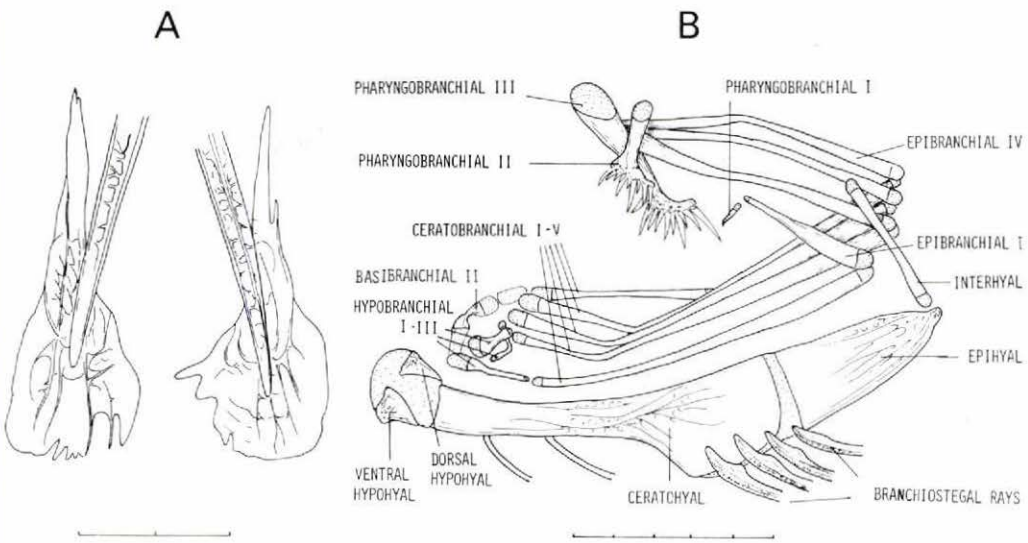

Fig. 2: A) Suboperculum of *Spiniphryne gladisfenae*, lateral views of right side and left side. B) Lateral view of hyoid apparatus and branchial arches of *Spiniphryne gladisfenae*. Full extend of branchiostegal rays not shown.

or projection, and irregularly notched unlike other ceratioids. The upper end of the suboperculum of the smallest known specimen of *Spiniphryne* (12.8 mm) is rounded as in adolescent specimens of *Oneirodes* (BERTELSEN, 1951: 77, Fig. 31).

d) *Branchial Arches* (Fig. 2 B)

There are three pharyngobranchials. A small, suspensory pharyngobranchial I is present; pharyngobranchials II and III are well-developed and bear teeth. The epibranchials and ceratobranchials are toothless. Hypobranchials II are well-developed and articulate directly with basibranchial II; hypobranchials III pass ventral to basibranchial II and approach each other on the midline. There are three basibranchials; only basibranchial II is ossified in the 49.0 mm specimen.

e) *Vertebrae, Caudal Skeleton, Unpaired Fins and Illicial Apparatus*

In the single cleared and stained specimen of *Spiniphryne* there are 20 vertebrae similar to those described for *Oneirodes* (PIETSCH, 1974: 12, Fig. 12). The hypural plate is unnotched posteriorly and bears the overlapping bases of nine principal caudal rays. These rays are all biserial and segmented. The third ray (from the top) through the sixth are bifurcated distally.

The dorsal fin consists of six biserial, segmented and unbranched rays. The proximal end of the first of six pterygiophores lies between the neural spines of the 10th and 11th pre-ural centra, while the proximal ends of the last two pterygiophores lie between the neural spine of the 7th and 8th pre-ural centra. The cylindrical, rodlike pterygiophore of the illicium, including its unossified posterior portion, is 33,7 percent of standard length.

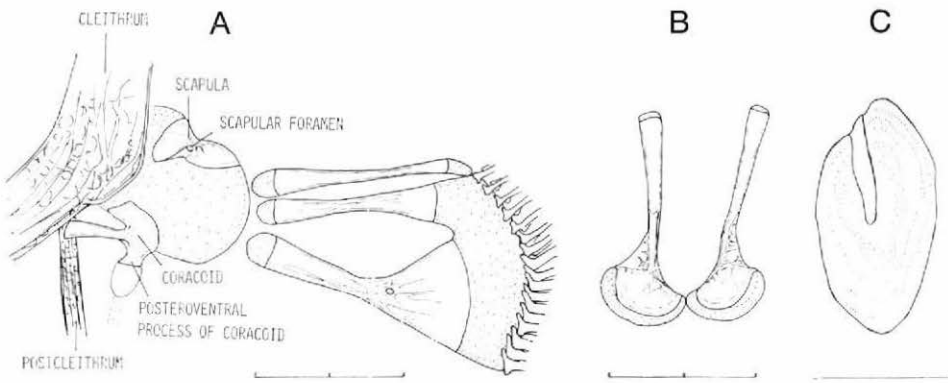

Fig. 3: A) Lateral view of portion of pectoral girdle and pectoral fin of *Spiniphryne gladisfenae*; left side. B) Anterior view of pelvic bones of *Spiniphryne gladisfenae*. C) Medial view of left sagitta of *Spiniphryne gladisfenae*.

The anal fin consists of four biserial, segmented and unbranched rays in the cleared and stained specimen (all other known specimens of *Spiniphryne* have five anal rays). The proximal end of the first pterygiophore lies between the haemal spines of the 9th and 10th pre-ural centra, the second between the haemal spines of the 7th and 8th pre-ural centra, and the third and last pterygiophore lies between the haemal spines of the 6th and 7th pre-ural centra.

f) *Pectoral Girdle, Pectoral Fin and Pelvic Bones* (Fig. 3 A, B)

The scapula is largely unossified and makes no bony contact with the cleithrum. A small scapular foramen is present near the ventral margin of the scapular ossification. A posteroventral process of the coracoid is present, the unossified tip of which is connected to the posterior margin of the postcleithrum by a ligament.

The pectoral fin lobe is shorter than the longest rays of the pectoral fin. There are three separate, well-ossified radials with no evidence that the lowermost is formed by fusion of two elements (as in *Centrophryne* and *Melanocetus*; PIETSCH, 1972: 41, Fig. 23). The broad, fused, cartilaginous distal ends of the lowermost radials support 15 to 17 movable fin rays. A small foramen is present near the middorsal margin of the lowermost radial.

The elongate pelvic bones are expanded distally and loosely connected to each other on the midline.

g) *Skin Spines*

Numerous, close-set skin spines covering the entire body and fins are visually obvious in uncleared specimens without microscopic aid.

h) *Otoliths* (Fig. 3 C)

The sagitta of *Spiniphryne* is very similar to that of *Oneirodes acanthias* (PIETSCH, 1972: 42, Fig. 24 (4)). The sulcus is deeply grooved, rostrum well-developed, antirostrum absent. The length to height ratio is 1.9 : 1. The ratio of SL of specimen to otolith length is 28.3 : 1.

Fig. 4: *Spiniphryne gladisfenae*, ISH 2734/71, 63.0 mm. (Drawn by *Elisabeth Anne Hoxie*)

D. Systematics

Genus *Spiniphryne* BERTELSEN, 1951.
Dolopichthys BEEBE, 1932: 86 (in part; type species *Dolopichthys allector* GARMAN, 1899, by original designation and monotypy).
Centrophryne REGAN and TREWAVAS, 1932: 84 (in part; type species *Centrophryne spinulosa* REGAN and TREWAVAS, 1932, hereby designated).
Spiniphryne BERTELSEN, 1951: 122, Fig. 81 (type species *Dolopichthys gladisfenae* BEEBE, 1932, by subsequent designation of PALMER and WHITE, 1953).
Bertelsenna WHITLEY, 1954: 30 (unacceptable replacement name for *Spiniphryne* BERTELSEN, 1951, therefore taking the same type species *Dolopichthys gladisfenae* BEEBE, 1932).

a) *Diagnosis*

An oneirodid that differs from all other genera of the family in having numerous, close-set skin spines covering the entire body and fins that are visually obvious without microscopic aid. In addition, *Spiniphryne* is unique in having the following combination of characters: dorsal profile of frontal bones convex; ventromedial extensions of frontals present; vomerine teeth present; nasal foramina circular; pterosphenoid present; pterygiophore of illicium emerging on snout between frontal bones with anterior end exposed, posterior end concealed under skin; illicium length greater than 10 percent of SL; lower jaw with a well-developed symphysial spine; sphenotic spines well-developed; articular spines rudimentary; angular spines absent; pharyngobranchial I present; pharyngobranchials II and III well-developed and toothed; epibranchials and ceratobranchials toothless; hypobranchial II present; posteroventral process of coracoid present; pectoral lobe short, shorter than longest rays of pectoral fin; posterior margin of operculum deeply notched; suboperculum short and broad, upper end rounded, lower portion semicircular in 12.8 mm adolescent specimen, elongate with upper end tapering to a point, lower portion circular and irregularly notched in larger specimens; anal fin with 4 or 5 rays.

Spiniphryne gladisfenae (BEEBE, 1932) (Textfigures 1, 2).
Dolopichthys gladisfenae BEEBE, 1932: 86—88 (original description; single specimen; holotype, USNM 170944 (originally New York Zoological Society 15490), 40.0 mm; Bermuda Oceanographic Expedition, Net 639, six miles south of Nonsuch Island, Bermuda; 700 fathoms; 28 May 1930).
Centrophryne gladisfenae REGAN and TREWAVAS, 1932: 84 (new combination; description after BEEBE, 1932).
Spiniphryne gladisfenae BERTELSEN, 1951; 75, 122, Fig. 81 (new combination; description after BEEBE, 1932; esca, suboperculum, pectoral radials, pelvic bone figured; in key).

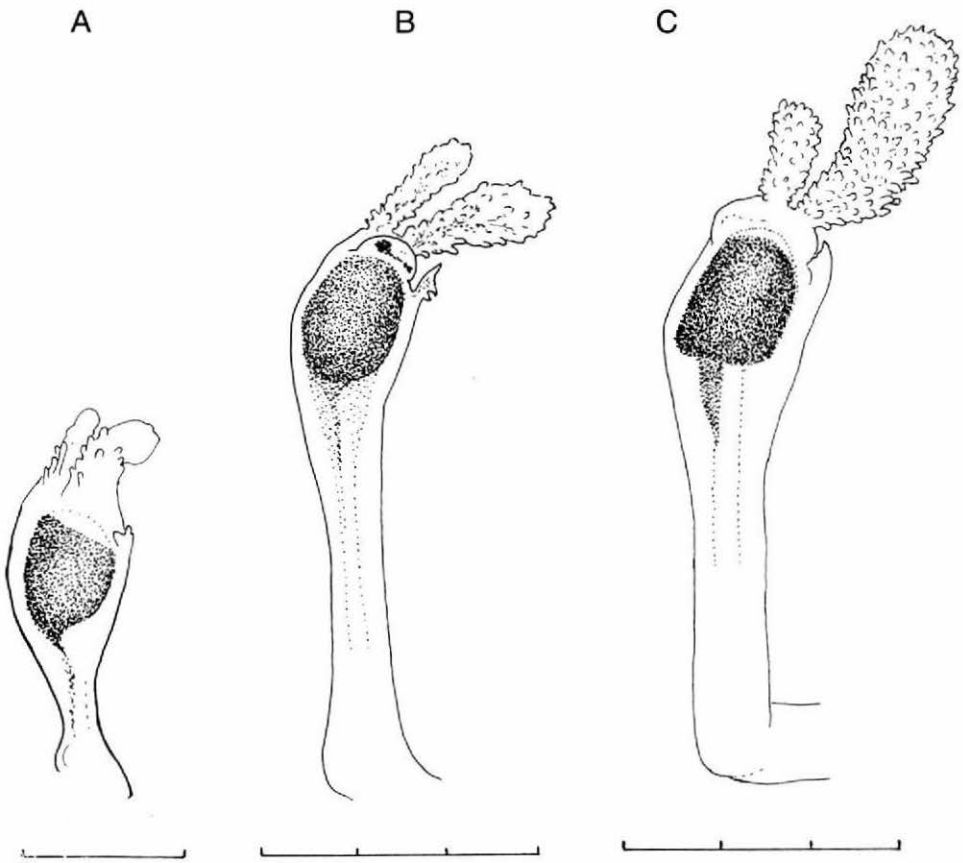

Fig. 5: Escae of *Spiniphryne gladisfenae*, left sides: A) IOS uncatalogued, 12.8 mm; B) ISH 2131/71; 49.0 mm; C) ISH 2734/71, 63.0 mm.

b) *Material examined:* 3 females, 12.8—63.0 mm

ISH 2734/71, 63.0 mm; "Walther Herwig" Station 494/71; 14° 05′ N, 23° 12′ W; CMBT—1600, 0—1900 m; 1942—2253 hr; 16 April 1971. ISH 2131/71, 49.0 mm; "Walther Herwig" Station 467/71; 5° 30′ S, 16° 28′ W; CMBT—1600, 0—1900 m; 1823—2225 hr; 9 April 1971.
IOS uncatalogued, 12.8 mm; "Discovery II" Station 8281—29; Rectangular Midwater Trawl 1, 0—1500 m; 17 March 1973.

c) *Description of Females*

Body elongate, slender, not globular; jaws equal anteriorly; lower jaw with a well-developed symphysial spine; oral valves well-developed, lining inside of both upper and lower jaws; hyoid barbel absent; two nostrils on each side at end of a single short tube; labial cartilage well-developed; eye subcutaneous, appearing through a circular, translucent area of integument; gill opening oval in shape, situated just posteroventral to pectoral lobe; ovaries paired.

Table 1 Counts, and measurements in percent of SL of *Spiniphryne gladisfenae*.

	IOS uncatalogued	ISH 2131/71	ISH 2734/71
Standard length	12.8	49.0	63.0
Length			
Head	29.7	29.6	31.0
Lower jaw	31.2	29 6	31.0
Premaxillary	18.0	20.4	22.2
Illicium	14.0	11.4	10.3
Operculum	15.6	19.4	19.5
Head width	23.4	17.6	15.9
Head depth	26.5	29.0	28.2
Teeth			
Upper jaw	23	40	42
Lower jaw	29	45	33
Vomer	2–2	3–2	3–3
Dorsal	6	6	6
Anal	5	4	5
Pectoral	15	17	15

Illicium length 10.3 to 14.0 percent of SL; esca with two distal appendages covered with small, digitiform papillae; and an unpigmented, tri-lobed posterior appendage (Fig. 5). According to observations on fresh, unpreserved specimens (E. BERTELSEN), the tips of the distal escal appendages were dark red and the posterior, tri-lobed appendage was bright, red-orange. No part of the esca was silvery. After 12 hours in formalin the coloration of the posterior remained unchanged while the distal appendages had become brown, probably indicating that the coloration was due to blood.

Teeth slender, recurved and all depressible, large and small intermixed in both jaws; teeth in lower jaw generally larger than those of upper jaw; number of teeth in upper jaw 23—42; lower jaw with 29 to 45; vomer with 2—3 teeth on each side.

Color in preservation dark-brown to black over entire external surface of body except for exposed part of pterygiophore of illicium, illicium and escal bulb (see description of esca above).

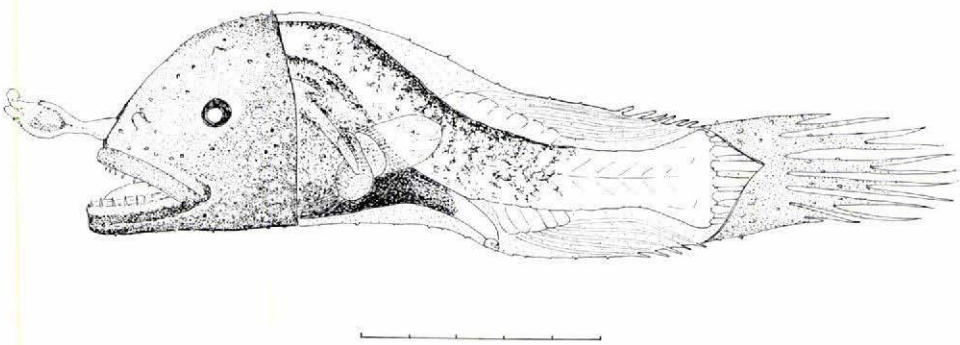

Fig. 6: *Spiniphryne gladisfenae*, IOS uncatalogued, 12.8 mm, showing pattern of inner pigmentation.

In the 12.8 mm adolescent specimen the subdermal pigmentation is well preserved (Fig. 6). The anterior part of the body musculature bears relatively well separated, large, branching melanophores more densely grouped along the back and extending posteriorly, slightly beyond the base of the dorsal fin. The fin bases and caudal peduncle are completely unpigmented. The peritoneum and gill cover are covered with a rather uniform pigmentation, without distinct groupings.

Counts, and measurements in percent of SL are given in Table 1.

d) *Males and larvae*

Unknown: Among the known oneirodid larvae, *Oneirodes*, *Lophodolos*, and the *Chaenophryne draco*-group lack pigment on the caudal peduncle as in the 12.8 mm, adolescent female specimen of *Spiniphryne*. In the shape of the suboperculum this specimen is similar to *Oneirodes* larvae, but differs distinctly from larvae of the latter two in which the upper end of this bone is slender and tapers to a point. Based on these characters, *Spiniphryne* larvae with only four anal fin rays may be confused with *Oneirodes*. They may, however, be distinguished by means of the size and density of the melanophores which are small and numerous in *Oneirodes* and larger and fewer in *Spiniphryne*. As the metamorphosed males can be expected to have spiny skin it should be possible to separate them from other oneirodid males on this character alone. Confirmation of the identification would be obtainable from the subdermal pigmentation, shape of the suboperculum, and in most cases the number of anal fin rays.

e) *Distribution*

Spiniphryne gladisfenae is known only from the Atlantic Ocean, three specimens collected from the eastern tropical Atlantic and the holotype from off Bermuda.

E. Evolutionary Relationships

The results of this study show that the phylogenetic position of *Spiniphryne* is clearly within the family Oneirodidae as diagnosed by Pietsch (1974: 30). Although, *Spiniphryne* and *Centrophryne* share a superficial resemblance in having a spinulose, elongate body, short head, and a horizontal position of the jaws, *Spiniphryne* and oneirodid genera exhibit a number of advanced osteological character states not found in *Centrophryne*. These include 1) three pectoral radials (four in Centrophryne); 2) absence of teeth on the ceratobranchials, 3) hypural plate entire (posteriorly notched in *Centrophryne*), 4) branchiostegal rays narrow and cylindrical (broad and compressed in *Centrophryne*), and 5) absence of an anterior, subopercular spine. Other characters that link *Spiniphryne* to the Oneirodidae to the exclusion of *Centrophryne*, but for which the relative primitiveness of states is unknown, include the following: 1) an anterodorsal keel of the ethmoid cartilage is absent (present in *Centrophryne*) 2) the space formed by the supraethmoid, the ventromedial extensions of the frontals, the prootics, and the parasphenoid is free of cartilage (cartilaginous in *Centrophryne*), 3) the sagitta of *Spiniphryne* (Pl. II, Fig. E) is morphologically much more similar to oneirodid sagittae than to that of *Centrophryne* (compare with Pietsch, 1972: 42, Fig. 24).

Within the family Oneirodidae, *Spiniphryne* is most phenetically similar and probably most closely related phylogenetically to *Oneirodes*. Based on the 30 osteological characters given by Pietsch (1974) in a study of evolutionary relationships among oneirodids, *Spiniphryne* and *Oneirodes* share a greater phenetic similarity than any other pair of genera, with 90 percent of their characters in the same state. Character states

unique to *Spiniphryne* and *Oneirodes* include the presence of 1) a posteroventral process of the coracoid, 2) skin spines, 3) a pharyngobranchial I, and 4) an anterior metapterygoid flange (character not used by PIETSCH, 1974). Although, *Spiniphryne* and *Oneirodes* share only three advanced character states (a reduction in the number of anal fin rays, and pectoral fin rays, and a reduction of the pelvic bone), all other known oneirodids share numerous, advanced states (see PIETSCH, 1974) that leave *Spiniphryne* and *Oneirodes* together at the base of oneirodid evolution. Of the two, *Spiniphryne* is more primitive. PIETSCH (1974) found *Oneirodes* to be the most primitive of nine oneirodid genera examined, exhibiting primitive states in 25 of 30 characters. *Spiniphryne*, however, is primitive in 27 of these same characters, being more primitive than *Oneirodes* in having rudimentary quadrate spines and a greater development of dermal spines. *Spiniphryne* is thus now considered to be the least derived oneirodid, most like the ancestral stock which gave rise to the family Oneirodidae.

F. Acknowledgements

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G. Literature

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