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A redescription of the lectotype of *Grimpoteuthis umbellata* (Octopoda: Cirrata: Grimpoteuthidae), and its taxonomic implications

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Abstract. *Grimpoteuthis umbellata* Fischer, 1893, the type species of the genus *Grimpoteuthis* Robson, 1932, the type genus of the family Grimpoteuthidae O'Shea, 1999, was described from 3 specimens (syntypes), 2 of which were damaged and 1 of which was a juvenile, collected in 1883 off the Azores (North Atlantic) between 1139 and 2235 m depth. Despite the systematic importance of this taxon, this species has remained poorly known. We re-describe the remnants of the extant, very damaged and since-designated lectotype to stabilize the concept of the species and genus, as part of an ongoing review of cirrate taxa. Of accepted North Atlantic congeners, *G. umbellata* is unique in lacking a radula and posterior salivary glands, and in having 8 lamellae per gill and web nodules positioned between suckers 27 and 31 along the arms. It differs from other adequately described species from the North Atlantic in combinations of various characters and their states. While we demonstrate that *G. umbellata* is most similar to *Grimpoteuthis discoveryi* Collins, 2003, we report certain characters and their states that serve to differentiate these 2 species. Further characters and their states are summarised for 6 grimpoteuthid taxa from the northeastern Atlantic to facilitate ongoing taxonomic revision of this and other deep-sea genera of finned octopus.

Key words. Taxonomy, systematics, cephalopod, cirrate octopus, deep-sea

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Introduction

The type genus of the cirrate octopus family Grimpoteuthidae O'Shea, 1999, *Grimpoteuthis* Robson, 1932, is one of 4 genera currently accepted in this family (the others being *Laetmoteuthis* Berry, 1913, *Luteuthis* O'Shea, 1999, and *Cryptoteuthis* Collins, 2004 (MolluscaBase Eds 2025)). Of these genera, *Grimpoteuthis* is the most species rich, containing 18 of the 22 currently accepted species in the family (MolluscaBase Eds 2025), and, because the type species of the genus is very imperfectly described, also one of the least known.

When Robson (1932) proposed the genus *Grimpoteuthis* he nominated the poorly known *Cirroteuthis umbellata* Fischer, 1884—the first described of the 12 named species that he attributed to *Grimpoteuthis* (rather than the best-known representative of it)—as the type species. Of these 12 species, 2 (as *G. mawsoni* (Berry, 1917) and *G. glacialis* (Robson, 1930)) were subsequently referred to *Cirroctopus* Naef, 1923 by O'Shea (1999), and then a new family, the Cirroctopodidae Collins & Villanueva, 2006 (Collins & Villanueva 2006); another (as *G. albatrossi* (Sasaki, 1920)) was referred to *Insigniteuthis* Verhoeff, 2024 as *I. albatrossi* Verhoeff (2025); *G. grimaldii* (Joubin, 1896) was referred to *Opisthoteuthis* Verrill, 1883; and a fifth, as *G. caudani* Joubin, 1896, was regarded as a junior synonym of *Opisthoteuthis grimaldii* (Joubin, 1896) by Villanueva et al. (2002). Almost 6 decades would elapse before any further species were described, with 11 species then added from 1990 to June 2025 (*G. bathynectes* Voss & Pearcy, 1990, *G. tuftsi* Voss & Pearcy, 1990, *G. abyssicola* O'Shea, 1999, *G. innominata* (O'Shea, 1999), *G. boylei* Collins, 2003, *G. discoveryi* Collins, 2003, *G. challengeri* Collins, 2003, *G. imperator* Ziegler & Sagorny, 2021, *G. angularis* Verhoeff & O'Shea, 2022, *G. greeni* Verhoeff & O'Shea, 2022, and *G. feitiana* Tang, Zheng & Zhang, 2025). Of these aforementioned 11 species, 7 (*G. boylei*, *G. challengeri*, *G. discoveryi*, *G. wuelkeri* (Grimpe, 1920), *G. umbellata*, *G. plena* Verrill, 1885, and *G. megaptera* Verrill, 1885) occur in the Atlantic, but

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only the first 4 of these are sufficiently known to enable any informed comparison (Collins 2003). While redescriptions of *G. plena* and *G. megaptera* are required to fully evaluate the diversity of *Grimpoteuthis* taxa in the North Atlantic, *G. umbellata* has nomenclatural priority over both (so its name will remain unaffected in the event revision deems either *G. plena* or *G. megaptera* to be a junior synonym).

The original description of *C. umbellata* was based on 3 different-sized syntypes described by the French malacologist Paul Henri Fischer (1835–1893) from the northeastern Atlantic. These specimens were collected during the June–August 1883 research cruise on the French vessel *Talisman*, a 75 m long steam-sail ship that sampled by dredge to nearly 5000 m depth along the northeastern Atlantic off Morocco, Senegal, Canary Islands, Azores, and near Sargasso Sea in the central North Atlantic (Dolan 2020). Following Paul Fischer's death, these 3 specimens were re-described and figured (Fig. 1A–G) by his son, the French malacologist Pierre Marie Henri Fischer (1865–1916) and the French malacologist Louis Joubin (1861–1935).

By 1995, only 2 syntypes remained (the large and small specimen) at the Muséum national d'Histoire naturelle (MNHN), Paris, France (Lu et al. 1995, Collins 2003); the whereabouts of the medium-sized syntype was unknown. Based on body shape and sucker form, Collins (2003) referred the small specimen (Fig. 1E–I) to *Opisthoteuthis* and designated the large specimen (which was missing its shell and most viscera) the lectotype. This rendered the other 2 specimens paralectotypes, regardless of whether they were congeneric or not. Because of the extensively damaged and incomplete nature of the lectotype, Collins (2003) could provide no detailed re-description of the lectotype; he did, however, proceed to describe 3 new taxa, and redescribe another. Consequently, no new taxon could be unambiguously differentiated from the type species of the genus, and the genus *Grimpoteuthis* could not be unambiguously differentiated from other genera in the Grimpoteuthidae. Despite this, without examining type material, Collins (2003) proposed the synonymy of *Enigmatiteuthis* O'Shea, 1999 with *Grimpoteuthis*; he subsequently described another genus, *Cryptoteuthis*, within the Grimpoteuthidae.

As part of a revision of South Pacific cirrate taxa, Verhoeff & O'Shea (2022) identified 3 of what they referred to as "groups" of *Grimpoteuthis* that shared certain combinations of characters and their states. The taxonomic status of these groups could not be resolved because the morphology of the type species of the genus (*G. umbellata*) was imperfectly known. To resolve this, and to facilitate further systematic reviews of *Grimpoteuthis* taxa, we here describe what we can from the fragmentary remains of the *G. umbellata* lectotype before it deteriorates further.

Materials and Methods

Measurements and abbreviations follow Verhoeff & O'Shea (2022), with additional abbreviations detailed in figure captions for gills and beaks. For the beaks, measurements and indices also follow Verhoeff & O'Shea (2022), with the ratios used being beak height as a percentage of beak width (H%W), beak height as a percentage of beak length (H%L), beak hood length as a percentage of beak length (HL%L), and, for the lower beak, the hood wing length as a percentage of beak length (WL%L).

Material examined

Lectotype. *Grimpoteuthis umbellata*, MNHN 3.6.698, sex indeterminate, northeast Atlantic, Azores, southwest of Ilha do Faial (Fayal)[1], 37° 55′ N, 029° 22′ W, 2235 m, *Talisman* Station (dredge) 130, 16.viii.1883 (the "large specimen" of Fischer & Joubin 1906).

Paralectotype. ?*Opisthoteuthis* sp., MNHN 3.6.699, sex indeterminate, northeast Atlantic, ~485 km northwest of Arguin sandbank, 23° 50′ N, 019° 37′ W; 1139 m, *Talisman* Station (dredge) 80, 11.vii.1883 (the "smallest specimen" of Fischer & Joubin 1906).

There is some uncertainty about the lectotype and paralectotype collection locality. Collins (2003: Table 1, 2) cited inconsistent coordinates and depths for both the above specimens; our cited collection details were cited by Fischer & Joubin (1906: 318) and verified by Aude Andouche (MNHN, June 2025). The lectotype was examined at the MNHN, Paris. The brachial crown, gills, buccal bulb, beaks, and pieces of intestine (some stored in a separate vial) were photographed (Canon 6D, 100 mm lens) after being blot-dried with tissue to minimize flash highlights.

Results

The original description of *Grimpoteuthis umbellata* by P. Fischer (1884) lacks detail and does not warrant repeating. The lectotype was more comprehensively redescribed by H. Fischer & Joubin (1906) [with simplified English translation] as:

[1]Fischer & Joubin (1906) described the location as "Açores, de Fayal à San Miguel" or "Azores, from Fayal to San Miguel" (i.e. along the ship's route as it headed through the Azores, approaching on a northeast course to Fayal, collecting the lectotype southwest of Fayal, before heading east and southeast towards and past São Miguel). This has been misinterpreted in some sources as "between Fayal and São Miguel," which is inconsistent with the coordinates.

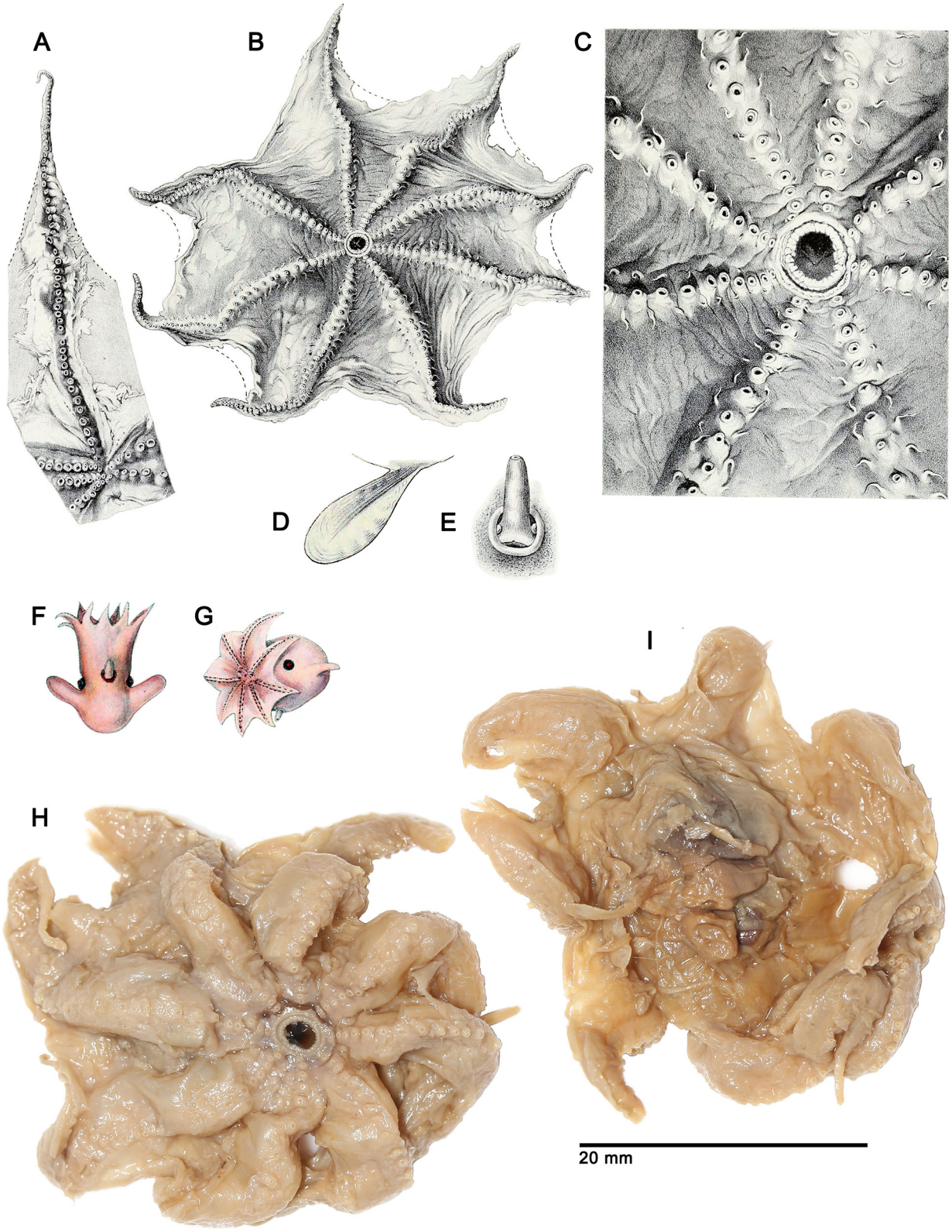

Figure 1. *Grimpoteuthis umbellata* type-series material. **A.** Only original illustration (lithograph) of the "plus grand échantillon" or "largest specimen" of FISCHER & JOUBIN (1906) (the lectotype; MNHN 3.6.698), oral aspect of one of the arms. **B–D.** The "échantillon moyen" or "medium-sized specimen" illustrated to show oral aspect of arms and webbing (**B**), close-up of suckers and cirri near the mouth (**C**), and one of the mantle fins (**D**). **E–I.** The "plus petit échantillon" or "smallest specimen" (MNHN 3.6.699; considered by COLLINS (2003) to be an *Opisthoteuthis*) depicting the funnel and pallial aperture (**E**), watercolour of the specimen in fresh condition in ventral (**F**) and lateral (**G**) aspects (watercolours made by the French zoologist Charles Jules Brongniart (1859–1899) of the specimen when live, aboard the *Talisman*), and oral (**H**) and aboral (**I**) aspects of the specimen in its present condition. Scale bars refer to H and I only. A–G were published by FISCHER & JOUBIN (1906) without scale bars, but "A" was life size or 1× scale (arm around c. 105 mm long), and the other images were scaled relative to 1× scale (B at 2× scale, C at 6× scale, D at 4× scale, E at 10× scale, F and G "slightly enlarged"). Lithographs A–E reproduced from FISCHER & JOUBIN (1906) pl. XXIII figs 1–5; F, G reproduced from FISCHER & JOUBIN (1906) pl. XXV figs 9, 10; photography (H, I) by Steve O'Shea, 2021.

> Le plus grand est en très mauvais état. Ni l'ombrelle ni les bras ne sont intacts; le sac viscéral manque complètement; … [The larger one is in very poor condition. Neither the web nor the arms are intact; the visceral sac is completely missing; …] (Fischer & Joubin 1906: 318)
>
> Il se réduit à la couronne brachiale, dont deux ou trois bras seulement sont complets; il reste une partie de l'épidérmie pigmenté en violet très foncé dans l'intérieur de l'ombrelle; cet épidérmie a complètement disparu à l'extérieur de l'ombrelle. Les bras intacts ont de 105 à 110 millimètres de long. Les cirrhes intercalés aux ventouses sont courts et peu distincts, en grande partie détruits. Le bras qui a été photographié (pl. XXIII, fig. 3) compte une soixantaine de ventouses distinctes, plus quelques autres très petites à l'extrémité, en tout de 65 à 68. Les ventouses, à partir de la huitième, ont acquis leur taille maximum; elles diminuent insensiblement à partir de la trentième. [It is reduced to the brachial crown, of which only 2 or 3 arms are complete; part of the epidermis, pigmented very dark purple, remains in the interior of the web; this epidermis has completely disappeared on the exterior of the webbing. The intact arms are 105–110 mm long. Cirri, intercalated with suckers, are short, indistinct, and largely destroyed. The arm that has been photographed (pl. XXIII, fig. 3) has about 60 distinct suckers, and a few very small ones at the end, 65–68 in all. Suckers, from the eighth onwards, have acquired their maximum size; they then decrease imperceptibly from the thirtieth.] (Fischer & Joubin 1906: 319)

Revised description of the lectotype

See Figures 2, 3; Table 1.

The specimen has deteriorated further. The remains comprise a brachial crown and arms, with remnants of the funnel, a buccal bulb with part of the oesophagus, beaks, intestine, and the gills (separated). Standard indices based on head width or mantle length cannot be computed/calculated, and, being absent, the fins and shell cannot be described; the optic nerves and reproductive system are absent.

The arms are approximately sub-equal in length and damaged, with the longest relatively intact arms 102–111 mm long (Fig. 2A, B). The dorsal and ventral arms were established based on the location of web nodules and buccal-bulb morphology. Maximum total arm sucker counts are arm IR (~68), arm IIR (~65), arm IIIR (~70), and arm IVR (~63); the proximal 5 or 6 of these are small, gradually increasing in diameter to sucker number ~7 or 8 (greatest diameter 2.0–2.2 mm), thereafter remaining comparably sized along the central portion of the arm (Fig. 2C) before subtly decreasing in diameter along the distal arm's third (from ~sucker number 30); they continue to the arm tips at minute size. Webbing is too fragmentary to estimate sector depths or web formula; a single web nodule occurs on the ventrolateral face of each of arms II–IV (those on arm pair I, if ever present, are now obliterated) positioned at the level of sucker 31 (II), 29 (III), and 27 (IV). Cirri commence on arms I between suckers 4 and 5, and on arms II–IV between suckers 3 and 4. The cirri are longest along the central portion of the arm, of similar length (2.0–2.7 mm) between suckers ~12 and 22 (0.9–1.35 × maximum (2.2 mm) sucker diameter), thereafter decreasing in length and continuing to arm tips at a minute size. The funnel is unremarkable, and the funnel organ (or vestige) is lost (Fig. 2D).

The gills are semi-sepioid with 8 or 9 lamellae (4 or 5 lamellae either side of the gill long-axis, and with anastomosed afferent vessels running along the "top" of the gill) (Fig. 3A, B). The proximal- and distal-most pairs of lamellae are smaller, and the distal pair have a common base.

The buccal bulb has been pre-dissected, with paired, small anterior salivary glands on the posteroventral face (separate from the buccal ganglia and with a single duct into the buccal bulb) (Fig. 3C). The posterior salivary glands are absent along the short length of the remnant oesophagus. The odontophore is present, without visible membrane or radular teeth (or vestige) under magnification. The labial palps (flanking the odontophore) are without palatine teeth.

The beaks have been previously dissected from the buccal bulb. The upper beak (Fig. 3D, E) is tall (H%L ratio 80%, H%W ratio 106.7%), the hood deep (HL%L ratio 65%), with the hood crest convex, the posterolateral edges slightly concave, and the rostrum sharp, deflected down, and with the jaw cutting edge straight; the lateral walls are near-parallel, each with a slight longitudinal groove, with the posterior edges near-straight; the crest is rounded. The lower beak (Fig. 3F, G) is tall (H%W ratio 60.6%), the hood is long (HL%L ratio 61.3%), with rounded crest and projecting rostrum with a sharp tip; the hood wings are long (WL%L ratio 112.5%); the lateral walls have a convex crest.

The stomach and digestive gland are absent. The caecum and fragmented intestine remain (3 pieces). The caecum appears to be uncoiled; it and the intestine have no distinctive feature (lacking anal flaps) (Fig. 3H).

Discussion

The missing medium-sized *Grimpoteuthis umbellata* paralectotype was described as being in better condition than the lectotype detailed herein, with at least 1 fin remaining. It was collected ~7 km north of the small paralectotype at 23° 52′ N, 019° 37′ W; 1250 m, *Talisman* Station 79, 11 July 1883 (Fischer & Joubin 1906). This specimen has been

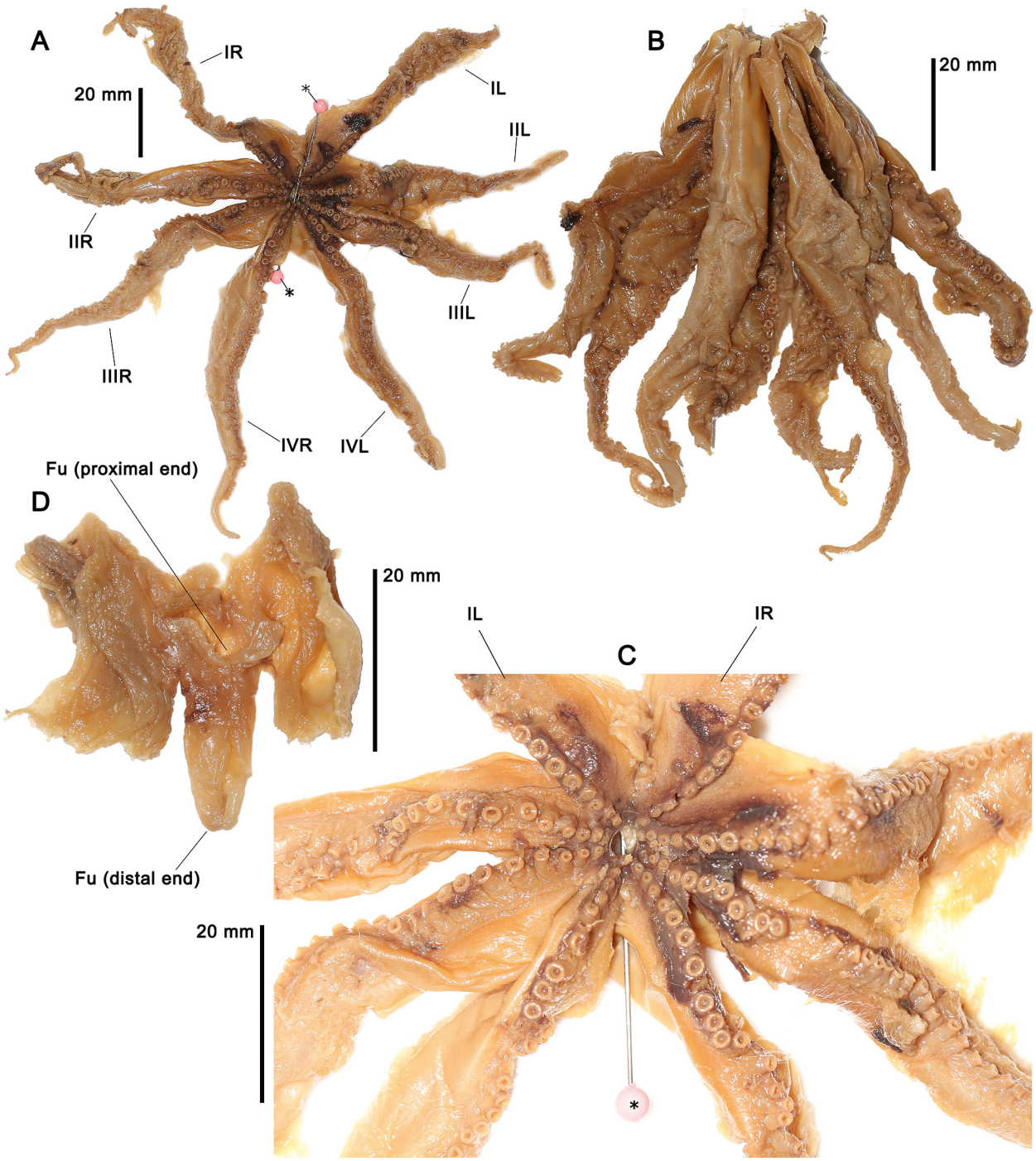

Figure 2. Arms, suckers, and funnel of the *Grimpoteuthis umbellata* lectotype, i.e. the large specimen (MNHN 3.6.698). **A.** Oral view of arms and suckers. **B.** Aboral aspect of arms. **C.** Close-up aspect of proximal suckers and cirri. **D.** Funnel and flanking sections of mantle tissue. Abbreviations: Fu = funnel; I–IV L or R = arms I–IV left or right. Photography by Steve O'Shea, 2021. Pins (marked by asterisk) were required to hold the specimen together for photographic/cosmetic purposes.

missing from the MNHN since at least 1995 (Lu et al. 1995, Collins 2003) and was not relocated during a more recent collection search (O'Shea pers. obs.). The third and smallest of the 3 specimens, the extant paralectotype was deemed to be non-congeneric by Collins (2003), who referred to it as a species of *Opisthoteuthis*. This specimen (Fig. 1H, I) certainly looks *Opisthoteuthis*-like today, yet the illustration of this same specimen, based on a watercolour of the live animal (Fischer & Joubin 1907: pl. XXV, figs 9, 10; see Figs 1F, G) resembles a juvenile *Grimpoteuthis* with its elongate mantle, and proportionally very large and laterally placed fins (comparable to juvenile *Grimpoteuthis* per Ziegler et al. (2021)); unfortunately the specimen has also been damaged and since it is very small (~30 mm across) we exercise restraint in not further dissecting it to reconstruct its anatomy, when this would be better undertaken when the comparative anatomies of these cirrate taxa are more completely understood.

Table 1. Measurements and counts for the *Grimpoteuthis umbellata* lectotype, i.e. the large specimen (MNHN 3.6.698), asterisk (*) indicates damage.

Measurement	
ML, TL, HW, FL, FW, EyD	NA
Funnel Length	19.8 mm
Arm length I (L/R)	86* mm / 102 mm
Arm length II (L/R)	98* mm / 105 mm
Arm length III (L/R)	90* mm / 106 mm
Arm length IV (L/R)	107* mm / 111 mm
Web nodule arm I (L/R)	No web nodules apparent on arms IR or L (damaged)
Web nodule arm II (L/R)	IIL at level of sucker 31 (59 mm along arm) / IIR (damaged)
Web nodule arm III (L/R)	IIIL (damaged) / IIIR at level of sucker 29 (61 mm along arm)
Web nodule arm IV (L/R)	IVL (damaged) / IVR at level of sucker 27 (63 mm along arm)
Sucker count arm I	IL: 38 intact suckers, 3 scars, tip broken (41+) IR: 47 intact suckers, scars for 6 more, tip stripped, scars/place for ~15 more suckers (~68)
Sucker count arm II	IIL: 48 intact suckers, scars for 8 more (+ 11 more suckers on tip in separate vial) (~67) IIR: 48 intact suckers, scars for 2 more, tip stripped, scars/place for ~15 more suckers (~65)
Sucker count arm III	IIIL: 43 intact suckers, scars for 3 more, tip broken (46+) IIIR: 41 intact suckers, scars for 3 more, tip stripped, scars/place for ~26 more suckers (~70)
Sucker count arm IV	IVL: 46 intact suckers R, tip stripped and broken, scars/place of ~9 more suckers (in total, ~54) IVR: 41 intact suckers R + 3 scars; tip stripped, scars/place for ~19 more suckers (in total, ~63)
Sucker diameter (# 7)	2.2 mm (IL) 2.0 mm (IIL) 2.0 mm (IIIL) 2.0 mm (IVL)
Cirri commence between suckers	4 & 5 (IL) 3 & 4 (II–IV L)
Cirrus length	2.7 mm (Collins 2003) 2.1 mm (sucker 16, IIIL) (similar length to sucker 21) 2.0 mm (sucker 12, IVL) (similar length to sucker 22, then reducing) (Cirri too damaged on arms I & II)
Gill lamellae counts (L/R)	8/9
Gill diameter	8.5 mm (Collins 2003)
Beak dimensions	Upper beak: BL (10.0 mm), BW (7.5 mm), BH (8.0 mm); HL (6.5 mm) Lower beak: BL (8.0 mm), BW (9.9 mm), BH (6.0 mm); HL (4.9 mm), WL (9.0 mm)
Other measurements	Anterior salivary glands, maximum dimension 1.9 mm Buccal bulb 11.0 mm long, 8.6 mm deep, 8.8 mm wide Remnant of intestine (with a loop) = 13.0 + 3.0 + 3.1 mm (~19.1 mm in total length)

Morphological comparison to North Atlantic grimpoteuthids

The buccal bulb of the *G. umbellata* lectotype lacks a radula, but an odontophore remains; while small anterior salivary glands are present, there is no trace of posterior salivary glands (or the duct that would connect to them, indicating that they were absent originally). This species shares the lack of a radula with *G. discoveryi*, and the lack of posterior salivary glands with *G. discoveryi* and *G. challengeri*. *Cryptoteuthis brevibracchiata* Collins, 2004 also lacks these structures, but it differs in its shorter arms, more proximal web-nodule positions, and shell morphology (Table 2). However, while obviously not conspecific with *G. umbellata*, the status of genus *Cryptoteuthis* requires further appraisal (the shell in particular resembles other species assigned to *Grimpoteuthis* and the presently synonymised *Enigmatiteuthis* (Verhoeff & O'Shea 2022)). Existing molecular analyses lack sufficient numbers of grimpoteuthid taxa, particularly *E. innominata* and *G. umbellata* (Verhoeff 2023), to properly resolve this.

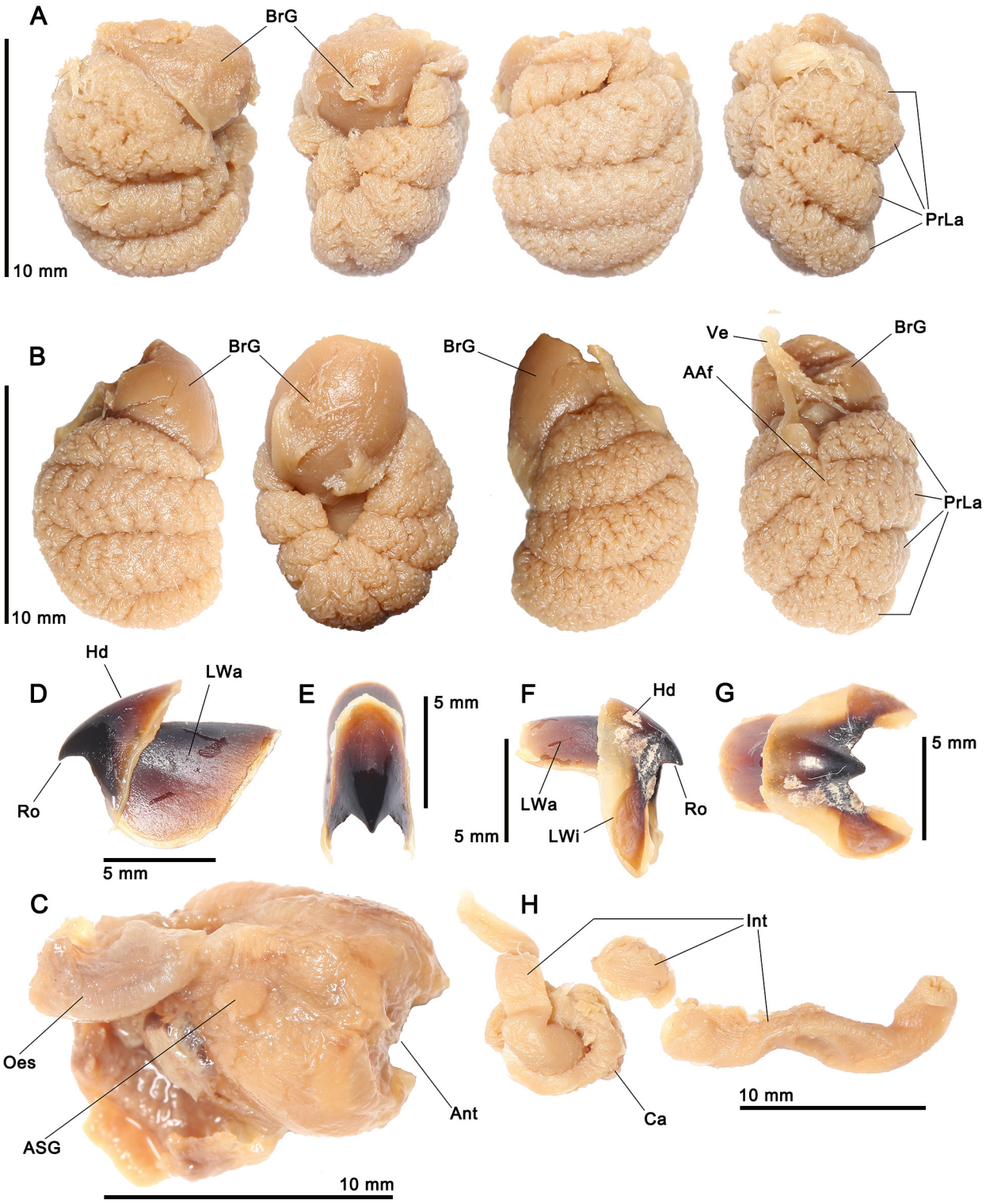

Figure 3. Gills and digestive tract of the *Grimpoteuthis umbellata* lectotype (MNHN 3.6.698). **A, B.** Gills: left (**A**) and right (**B**), left–right being rotations around each gill (each separated with the old attachment point at top, distal lamellae lowermost). **C.** Buccal bulb and partial oesophagus. **D**, **E.** Upper beak: lateral (**D**) and anterior (**E**) aspects. **F**, **G.** Lower beak: lateral (**F**) and ventral (**G**) aspects. **H.** Damaged pieces of the intestine and caecum. Abbreviations: AAf = anastomosed afferent vessel; Ant = anterior end (of buccal bulb); ASG = anterior salivary gland; BrG = brachial gland; Ca = caecum; Hd = hood (of beak); Int = intestine; LWa = lateral wall (of beak); LWi = lateral wing (of beak); PrLa = primary lamellae; Oes = oesophagus; Ro = rostrum; Ve = blood vessels. Photography by Steve O'Shea, 2021.

The *G. umbellata* lectotype upper beak (Fig. 4) is particularly interesting because its H%W ratio and that of *G. discoveryi* are very similar (106.7% vs 105%) (Table 2); this ratio differs for other species (88.6% for *C. brevibrachiata*, and 113.6%–134% for *G. boylei*, *G. challengeri*, and *G. wuelkeri*). The upper beaks of *G. boylei* and *G. chal-*

lengeri are more elongate than those of other species (including *G. umbellata*). The upper beak HL%L ratio, and flat posterior face of the lateral walls of *G. umbellata* are similar to those of all northeast Atlantic *Grimpoteuthis*, excepting *G. wuelkeri*. While differences in lower beak measurements could be an artefact of measurer technique between studies, we do not believe so because the (illustrated) beaks of no other North Atlantic *Grimpoteuthis* taxon resemble those of the (photographed) *G. umbellata* lectotype beaks (Fig. 4). The lower beak of *G. umbellata* is quite unlike that of any other North Atlantic *Grimpoteuthis* taxon.

Grimpoteuthis discoveryi material examined by Collins (2003) had 7 lamellae per gill on most (29) specimens, but 8 lamellae on either both gills (4 specimens) or at least 1 of them (10 specimens), and even 6 lamellae (3 specimens). While these values overlap with gill lamellae counts for *G. umbellata*, both *G. boylei* and *G. challengeri* also have 8 lamellae per gill, and *G. wuelkeri* and *C. brevibracchiata* have 6 or 7 lamellae per gill. Thus, gill lamella counts may be of limited value for distinguishing grimpoteuthid taxa.

Aspects of web-nodule position, cirrus starting points and length, and arm-sucker count (ASC) values of northeastern Atlantic grimpoteuthid taxa are presented in Table 2. Cirri in *G. umbellata* commence between suckers 3 and 5, and in *G. discoveryi* between suckers 4 and 5; in *G. boylei*, *G. challengeri*, and *G. wuelkeri* these commence between suckers 5 and 7. Maximum cirrus length in *G. umbellata* (0.9–1.35 × sucker diameter) and *G. discoveryi* (1.0–2.0×) and *G. wuelkeri* (0.8–2.5×) are similar, whereas *G. boylei* and *G. challengeri* tend to have longer cirri (1.3–3.6× and 2.4–5.4×, respectively). Excepting *G. wuelkeri*, which has more proximal web nodules, web-nodule

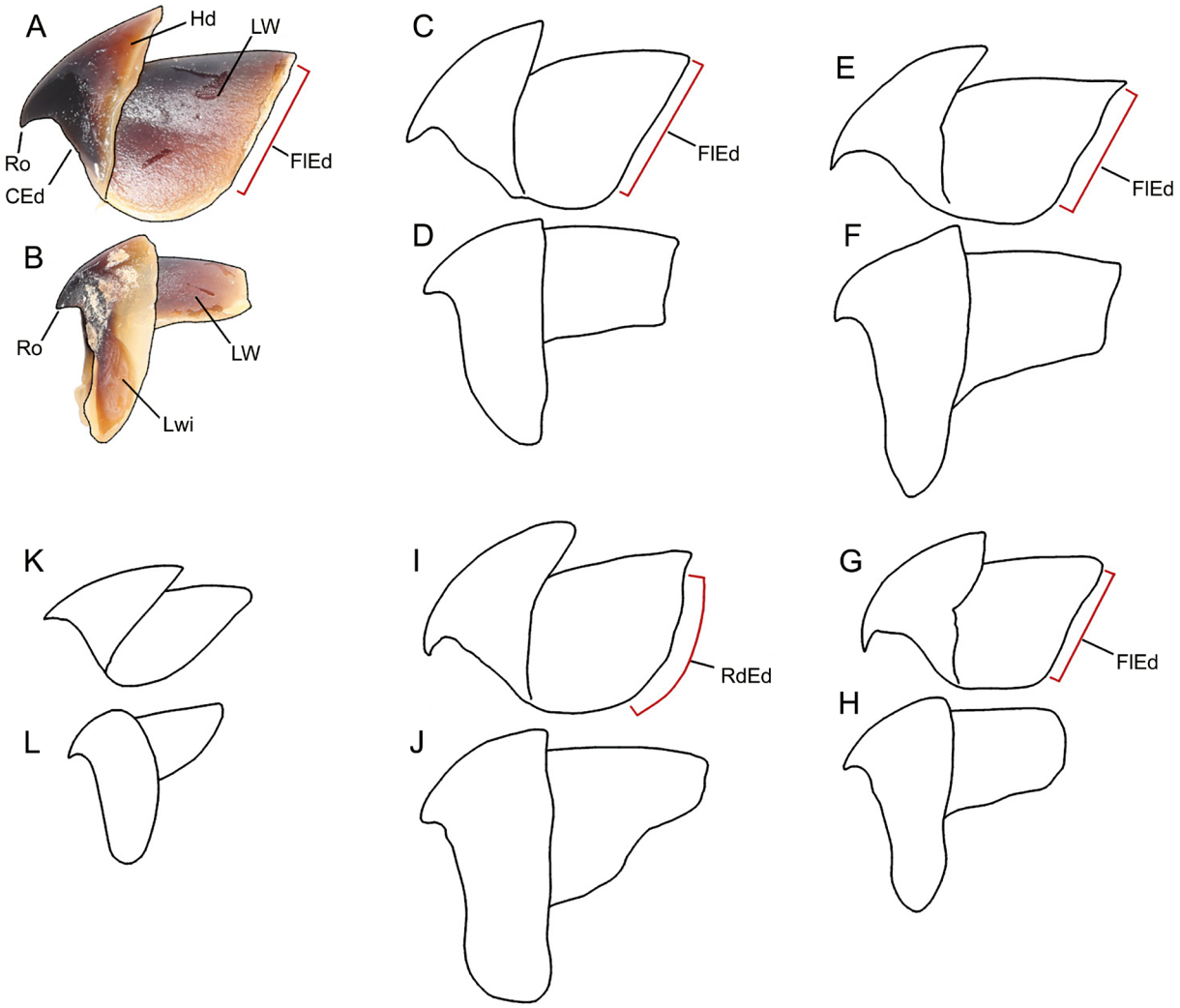

Figure 4. Beak comparison of *G. umbellata* lectotype beaks to beaks of northeastern Atlantic grimpoteuthidid taxa. **A, B.** *G. umbellata* lectotype: upper (**A**) and lower (**B**) beaks. **C**, **D.** *G. discoveryi*: upper (**C**) and lower (**D**) beaks. **E**, **F.** *G. challengeri*: upper (**E**) and lower (**F**) beaks. **G**, **H.** *G. boylei*: upper (**G**) and lower (**H**) beaks. **I, J.** *G. wuelkeri*: upper (**I**) and lower (**J**) beaks. **K**, **L.** *C. brevibracchiata*: upper (**K**) and lower (**L**) beaks. C–J redrawn from Collins (2003) figs 5d, 9d, 12d, 15c; K and L redrawn from Collins (2004) fig. 4d. Abbreviations: CEd = cutting edge (of jaw); FlEd = flat edge (of posterior lateral walls); Hd = hood; LW = lateral walls; LWi = lateral wings (of hood); RdEd = rounded edge (of posterior lateral walls); Ro = rostrum. All these beaks are a similar size (~10 mm across).

positions of other northeastern Atlantic *Grimpoteuthis* are similar. Reconstructed ASC values (which include counts of scars) for the lectotype of *G. umbellata* (67–70 for arms II) are consistent with ASC values reported by FISCHER & JOUBIN (1906) for this same specimen (65–68) when it was in better condition; these counts differ most notably from those of *G. discoveryi* (57–61), and the 2 species also differ in beak morphology (Table 2).

Range and bathymetric comparisons

The *G. umbellata* lectotype was collected southwest of the Azores Archipelago (37°55′N, 029°22′W) at 2235 m depth. From data provided by COLLINS (2003) for bathymetric ranges (for at least a dozen specimens per species), *G. boylei* and *G. challengeri* occur at greater depth (4190–4847 m and 4800–4850 m, respectively), *G. discoveryi* occurs from 2600 to 4870 m, and *G. wuelkeri* from 1550 to 2056 m (an attribution of *G. wuelkeri* from 5430 m in Angola Basin, South Atlantic, by PIATKOWSKI & DIEKMANN (2005) cannot be reliably attributed to this species). COLLINS (2003) reported each species to have a relatively large range through the northeastern Atlantic, with *G. wuelkeri* and *G. challengeri* also occurring in the northwestern Atlantic. Only *G. discoveryi* was collected from near the Azores (specifically Bergen University Museum, Norway, ZUB 36379, 34°59′N, 033°01′W, 2615 m; and Musée océanographique de Monaco, MOM 295091, 39°54′N, 020°27′W, 4360 m), relatively close to the *G. umbellata* type locality.

Conclusion

COLLINS (2003: 93) remarked how the *G. umbellata* type material was "… in such poor condition that comparison with recently captured material was not possible". We agree that it is in very poor condition, but we can augment its description and detail further morphological features that facilitate comparison with other northeastern Atlantic taxa. Notably, we report the beaks, buccal mass, and

Table 2. Comparisons of North Atlantic Grimpoteuthidae morphology, including data for species from COLLINS (2003, 2004). Values for a single specimen (*G. umbellata* and *C. brevibracchiata*) are compared with ranges across many specimens for other species. Cells shaded orange indicate differences from the *G. umbellata* lectotype (i.e. the large specimen). *Grimpoteuthis plena* and *G. megaptera* are too poorly known for comparison. Delta symbols (Δ) for upper beak indices indicate percentage difference relative to *G. umbellata* lectotype

Feature	***G. umbellata* Lectotype**	***G. discoveryi***	***G. boylei***	***G. challengeri***	***G. wuelkeri***	***C. brevibracchiata***
Radula	No	No	Yes	Yes	Yes	No
Posterior salivary gland (present)	No	No	Yes	No	Yes	No
Web-nodule position	31 (arm II) 27–29 (III & IV)	29–31 (I & II) 25–27 (III & IV)	28–31 (I & II) 24–25 (III & IV)	30–34 (I & II) 27–28 (III & IV)	26–28 (arm I & II) 22–24 (III & IV)	23–25 (I & III) 22–23 (III & IV)
Sucker counts	67–70 (arms I & II)	57–61	55–58	63–72	60–70	45–48 (1 specimen)
Max cirri length relative to sucker diameter	0.9–1.35× sucker diameter	1.0–2.0	1.3–3.6	2.4–5.4	0.8–2.5	1.67
Cirri start point	3 & 5	4 & 5	5–7	5–7	5 or 6 (rarely 4–7)	2 & 3
Gill lamellae	8/9	6–8	7 or 8	8	6 or 7	7
Upper beak H%W	106.7%	105.0% (Δ1.7%)	122.6% (Δ15.9%)	134.0% (Δ27.3%)	113.6% (Δ6.9%)	88.6% (Δ18.1%)
Upper beak HL%L	65.0%	62.5% (Δ2.5%)	66.5% (Δ1.5%)	63.8% (Δ1.2%)	69.3% (Δ4.3%)	70.3% (Δ5.3%)
Upper-beak postero-ventral edge shape	Flat	Flat	Flat	Flat	Convex	Flat
Lower beak H%W	60.6%	76.6%	68.5%	68.4%	67.8%	62.8%
Lower beak HL%L	61.3%	54.1%	55.3	53.8%	52.9%	47.3%

web-nodule positions. Overall, of described northeastern Atlantic grimpoteuthid taxa, the lectotype of *G. umbellata* is most similar to *G. discoveryi* (lack of a radula, where the cirri commence along the arms, and upper beak H%W ratio). It resembles *G. challengeri* also in lacking posterior salivary glands, both *G. discoveryi* and *G. wuelkeri* in cirrus length, and all northeastern Atlantic *Grimpoteuthis* excepting *G. wuelkeri* (i.e. *G. boylei*, *G. challengeri*, and *G. discoveryi*) in web-nodule position, gill-lamellae counts, upper-beak HL%L ratio, and upper-beak posterior-edge shape. The bathymetric range of *G. umbellata* falls within the recognised range of both *G. discoveryi* and *G. wuelkeri*, but only *G. discoveryi* has been collected from near the type locality of *G. umbellata*. That said, the pronounced differences in lower beak morphology and ASC values lead us to believe that *G. umbellata* and *G. discoveryi* are distinct species. Further *Grimpoteuthis* material collected near the Azores from (nominally) 1700–2500 m depth must be compared directly with the *G. discoveryi* holotype to more fully appraise relationships between these 2 taxa.

Of the 3 groups of *Grimpoteuthis* taxa referred to by Verhoeff & O'Shea (2022), the *G. umbellata* lectotype is most similar to "Group 1." *Grimpoteuthis* Groups 1 and 3 have a shell with well-developed saddle "shoulders" and lobe-like lateral shell wings with a distinctly offset, spike-like projection from the ventral edge (a feature seen in both *Enigmatiteuthis* and *Cryptoteuthis*, which may belong to one of these groups). Group 2 taxa lack shell saddle "shoulders", and the wing ends are simple rounded lobes (*G. abyssicola* and *G. hippocrepium* (Hoyle, 1904)). In addition to establishing the relationship between *G. umbellata* and *G. discoveryi*, future work will need to focus on acquiring molecular data (especially COI sequencing) for representatives off all 3 of these groups, including representatives of *Enigmatiteuthis* and *Cryptoteuthis* to clarify the synonymy of these deep-sea forms that are rarely represented in collections. We might add that the type series of *G. umbellata* was almost certainly fixed in alcohol aboard the *Talisman* (Milne-Edwards 1884: 227), though its subsequent treatment history is unknown (specifically, if any specimen has been subsequently exposed to formaldehyde); we have not taken a tissue sample for attempted sequencing.

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