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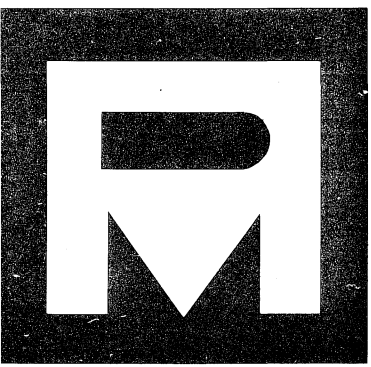
CHARLOTTE P. MANGUM
WILLIAM R. RHODES



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THE TAXONOMIC STATUS OF QUILL WORMS, GENUS HYALINOECIA (POLYCHAETA: ONUPHIDAE), FROM THE NORTH AMERICAN ATLANTIC CONTINENTAL SLOPE

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ABSTRACT

Morphological characters of quill worms from the North American continental slope have been compared with those of *Hyalinoecia tubicola* (O. F. Müller) from the English Channel. The results indicate consistent and exclusive differences in worms of the same size. We suggest that *Hyalinoecia artifex* Verrill be reinstated for North American quill worms, as originally intended.

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INTRODUCTION

Quill worms of the onuphid genus *Hyalinoecia* are often dredged in great numbers from 400–1500 meters depth on the continental slope of the northwestern Atlantic Ocean. These worms were originally described as *H. artifex* by Verrill (1880, 1885a, 1885b), who remarked upon the close relationship with the European *H. tubicola* (O. F. Müller). The primary difference clearly stated by Verrill (1880) is larger size, although his full description (Verrill, 1885b) includes a number of morphological characters that do not agree with those of *H. tubicola.*

Probably unaware of Verrill's findings, Ehlers (1887) described a North American collection of extremely small (less than 21.5 mm long) worms as *Onuphis gracilis,* explicitly noting the resemblance to both *H. tubicola* and the West Indian *H. varians* Baird. Quite a few characters, notably the condition of the occipital antennae, the anterior setae and the absence of so-called "Augenflecke" on the largest specimen, do not agree with *H. tubicola.*

Augener (1906) noted the existence of differences between European and American worms, particularly the absence of "eyes" and the location of gills, but nevertheless synonomized both *H. artifex* Verrill and *O. gracilis* Ehlers with *H. tubicola* (O. F. Müller). He believed that the differences could be attributed to size.

Since Verrill's discovery of a North American quill worm, other animals identified as *H. tubicola* have been dredged from all of the world's major seas except the Antarctic Ocean. The species is often cited as an example of the cosmopolitan fauna of the deep sea (Ekman, 1953). The concept of a single faunal assemblage comprised largely of cosmopolitan species inhabiting the depths of oceans throughout the world is currently being questioned due to the elucidation of distinct faunas in different regions (Sanders, Hessler and Hampson, 1965). Nonetheless, there remains a sizable group of species such as *H. tubicola* that have been so widely reported that they are considered cosmopolitan. We have investigated American and European representatives of this species in hopes of clarifying the basis of morphological differences noted by earlier workers. Diagnoses of morphological, physiological and molecular characters will be presented in evidence. This paper is restricted to a morphological comparison of three populations, one European and two North American.

All animals in our own collections were removed from their

tubes prior to preservation in 70% ethyl alcohol. This precaution not only facilitates preservation but also prevents autotomy of the tail region and distortion of the body. We made no special effort to insure against bias for size; the measurements given are intended to portray the samples on which our results are based, not the natural populations. The error is probably not large, but small worms are easily overlooked in shipboard sorting, and a few of the largest were discarded from the European sample because they did not fit the mailing containers.

RESULTS

European worms

Hyalinoecia tubicola (O. F. Müller, 1776)

Hyalinoecia tubicola Quatrefages, 1865; Grube, 1878; Langerhans, 1880; Fauvel, 1923; Støp-Bowitz, 1948.

More than 300 specimens were collected by R/V *Sula* of the Marine Biological Association of the United Kingdom in the summer of 1967. The worms originated from depths of 44 to 55 meters in the English Channel (50° 15–17′ N, 4° 20–30′ W). Excluding tentacles and terminal cirri, the size range of the animals was 35–130 mm (Fig. 1A). The quill-like tubes of the species, a few cm longer than their inhabitants, were described by Watson (1903).

DESCRIPTION OF MATERIAL COLLECTED. Prostomium bulbous, bearing five occipital antennae with annulate (3–4 rings) ceratophores, and two stout, short frontal antennae without ceratophores. Three dorsomedial occipital antennae of equal length, twice as long as more lateral pair (Fig. 166i in Fauvel, 1923), and extending posteriorly as far as setigerous segment XVI. Two dark pigment spots (often designated "eyes" in the literature) occurring lateral to the bases of the dorsomedial paired occipital antennae. Ventrally two large globose palps forming the upper border of the mouth.

Buccal segment dorsally forming an achaetous ring at the base of the prostomium. Mouth located ventrally, with reniform lower lip and two protruding wing-shaped mandibles. Four pairs and one unpaired dark maxillae (Fig. 88 in McIntosh, 1885). Maxillae I hooked forceps. Right maxilla II typically with 13–14 teeth (range

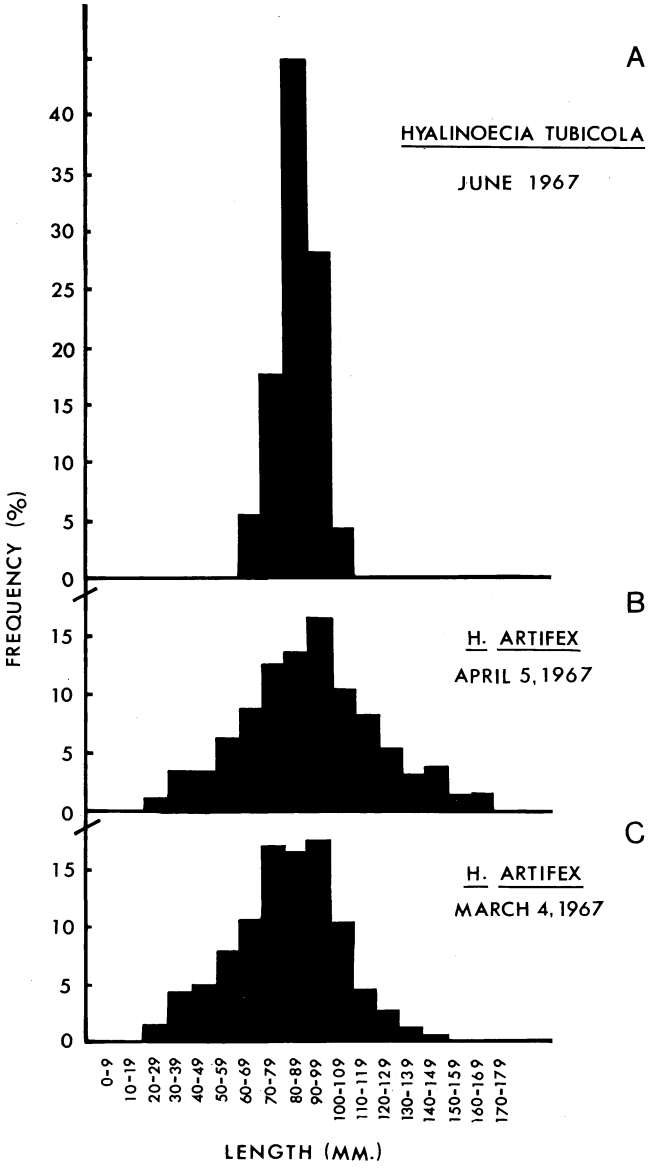

FIG. 1. Size distribution in sample of quill worms. A. English Channel. B. and C. North American continental slope (420–480 m).

10–15); left maxilla II with 12 (11–14) teeth. Right maxilla III absent; left maxilla III with 13 (12–14). Right maxilla IV with 10 (10–11); left with 13 (12–14). Each right and left maxilla V with 1 tooth only.

Setigerous segment I smooth dorsally, longer than succeeding segment. Parapodia enlarged, directed anteroventrally. Dorsal parapodial cirri about same size as on segment II; ventral cirri slightly larger than on II. Presetal lobe somewhat fan-shaped (enlarged distally) covering the bases of typically 3 (2–6) stout tridentate acicula (Fig. 2A). Postsetal lobe cirriform, about one-half as large as on setiger II.

Setigerous segment II shorter than I. Parapodia smaller, more conical and directed ventrally. Presetal lobe spatulate, covering bases of 2–4 bilimbate capillary setae (Fig. 2D in Claparède, 1868) which are noticeably stouter than in succeeding segments, 2–4 stout tridentate acicula and a small clump of pectinate setae. Postsetal lobe more closely applied to fascicle, less conical, and more lobulate than on I.

Setigerous segment III closely resembling II though slightly smaller. Dorsal and ventral parapodial cirri slightly smaller than on II, beginning posterior gradation in size. Limbate capillary setae

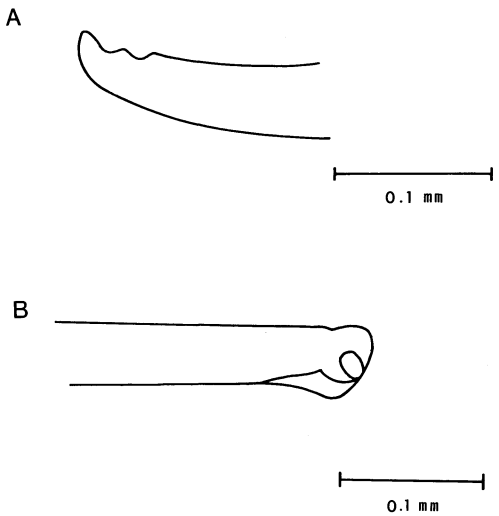

FIG. 2. *Hyalinoecia tubicola* (O. F. Müller). English Channel. A. Tridentate aciculum from setiger I. B. Hooded bidentate aciculum from branchial region.

up to 11; clump of pectinate setae in dorsal portion of fascicle. Emergent acicula lacking.

Setigerous segment IV with several pectinate setae (Fig. 166n in Fauvel, 1923) as well as limbate capillaries. Ventral cirrus short, globose, becoming a flattened cushion by setiger V and persisting as such for rest of body length. Presetal lobe diminishing to rudimentary lip on branchial segments. Postsetal lobe diminishing to rudimentary lobe, then disappearing by setiger XXXV.

Branchiae flattened, beginning typically at setiger XXIV (XXIII to XXV) and subsequently increasing in length up to or more than two-thirds the body width. Dorsal parapodial cirri simultaneously decreasing to a fine filament about one-tenth the length of the branchial filaments.

Number of limbate setae increasing to maximum of 14 per fascicle between setigers IX to XXV. Single hooded bidentate aciculum (Fig. 2B) appearing in the middle of the fascicles at about setiger XXV (XX to XXVIII), increasing to typically 2–3 (up to 5) more posteriorly. Hooded bidentate aciculum notched immediately proximal to teeth, which are directed at acute angle to main axis of seta (Fig. 2B). Number of limbate capillary setae decreasing to 9 or less per fascicle in the midbranchial region. Pectinate setae present on all but setiger I. Three stout, tapered, hooded acicula present internally in all parapodia but typically not emerging.

Posterior region becoming flattened, ending in large pygidium with two fragile terminal cirri. Last few segments without branchiae but with dorsal cirri and all setae types (in reduced numbers).

Material deposited in the Peabody Museum, Yale University, YPM No. 2694.

North American worms

Hyalinoecia artifex Verrill 1880

Hyalinoecia artifex Verrill, 1885a; Verrill, 1885b.
Onuphis (Paronuphis) gracilis Ehlers, 1887.
Hyalinoecia tubicola Augener, 1906; Hartman, 1944; Pettibone, 1963.

We have collected thousands of specimens from the Atlantic continental slope at 420–480 meters depth, 34° 16′ N, 75° 48′ W. The collections were made on cruises on R/V *Eastward* of the

Duke University Marine Laboratory in the period 1965–68. The description below summarizes our examination of several hundred worms ranging in length from 15 to 180 mm (Figs. 1B and 1C). The morphology is stable after the worms reach a length of approximately 20 mm, but quite plastic in smaller animals. The description pertains to worms exceeding 20 mm; a few notes on juvenile specimens follow at the end.

DESCRIPTION OF MATERIAL COLLECTED. Prostomium bulbous (Fig. 3A), bearing five occipital antennae with annulate (3–4 rings) ceratophores and two short, stout, frontal antennae without cerato-

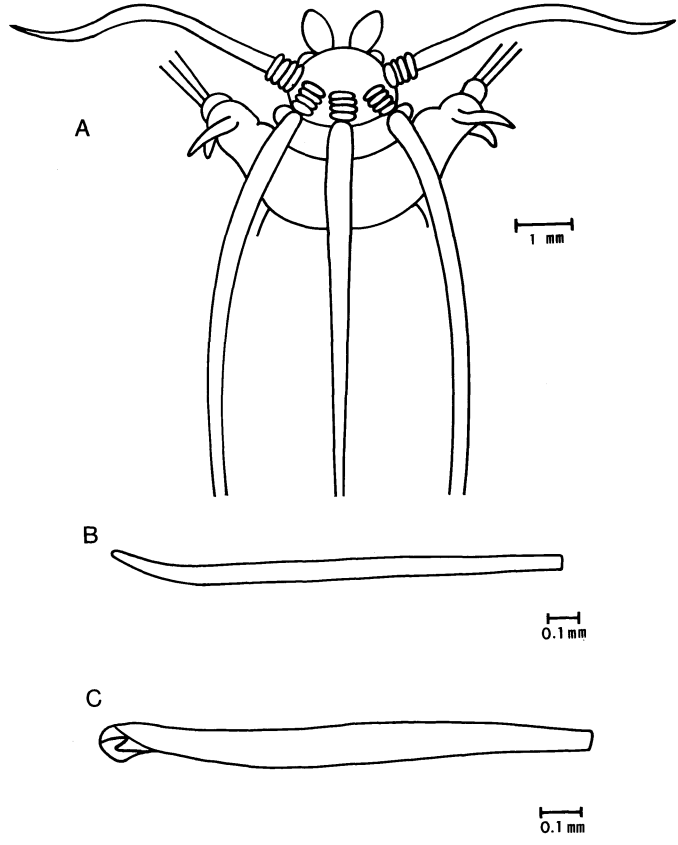

FIG. 3. *Hyalinoecia artifex* Verrill, continental slope (420–480 m). A. Anterior region, dorsal view. B. Blunt aciculum from setiger I. C. Hooded bidentate aciculum from branchial region.

phores. Three dorsomedial antennae of equal length, about 3–4 times the length of the more lateral pair (Fig. 178 in Verrill, 1885b) and extending as far posteriorly as setiger XXX. Prostomium of adult worms invariably without dark pigment spots (see notes on juvenile specimens below). Ventrally two large globose palps forming upper border of mouth.

Buccal segment dorsally forming achaetous collar at base of the prostomium. Mouth located ventrally, with reniform lower lip and two protruding wing-shaped mandibles. Four pairs and one unpaired maxillae; Maxillae I hooked forceps; right maxilla II with 13 (10–15) teeth; left with 14 (11–16). Right maxilla III absent and left with 13 (11–15) teeth. Right maxilla IV with 12 (9–14) and left with 10 (8–12). Each maxilla V with 1 tooth only.

Setigerous segment I smooth dorsally, longer than succeeding segment. Parapodia enlarged, directed anteroventrally: Dorsal and ventral parapodial cirri smaller than on setiger II. Presetal lobe somewhat fan-shaped (enlarged distally) covering bases of 3–4 stout, smooth-tipped acicula (Fig. 3B). Postsetal lobe cirriform, about one-half as large as on setiger II.

Setigerous segment II slightly shorter than I. Parapodia smaller and more conical than on I, directed ventrally. Dorsal and ventral cirri larger than on I. Presetal lobe spatulate, covering bases of 3–4 stout acicula, 3–4 stout mono- and bilimbate capillary and small clump of pectinate setae. Postsetal lobe closely applied to fascicle.

Setigerous segment III slightly smaller than II. Dorsal cirri longer than on II; ventral parapodial cirri smaller than on I, beginning to diminish and becoming very small in mid-branchial region (see below). Presetal lobe a small tongue, beginning to diminish. Postsetal lobe similar to that on II, but beginning to diminish. Limbate capillary setae up to 10; clump of pectinate setae in dorsal portion of fascicle. Emergent acicula lacking.

Setigerous segment IV with slightly smaller parapodia than III; parapodia diminishing to roughly constant size by VII. Pectinate setae present, as well as limbate capillaries. Ventral cirrus short, globose, becoming a flattened cushion by VII. Presetal lobe grading to rudimentary lip by setiger X and persisting as such posteriorly. Postsetal lobe beginning gradation to rudimentary lobe by setiger L.

Branchiae simple, flattened, beginning typically at setiger XXIX (XXVI to XXXIII); length up to but not exceeding two-thirds of

body width. Dorsal parapodial cirrus decreasing to fine filament at base of branchiae and about one-eighth the length of the branchial filament; dorsal cirrus becoming somewhat larger again in post-branchial region.

Maximum number of limbate setae about 16, occurring between setigers XV and XL. Single hooded bidentate aciculum appearing in center of fascicle between setigers XXIV and XLV, increasing to 2 (uncommonly 3) in more posterior segments; hooded acicula not notched, with teeth directed parallel to main axis (Fig. 3C). Number of limbate capillary setae decreasing to maximum of 12 in mid-branchial region. Pectinate setae present on all but setiger I. Three stout, tapered, hooded acicula present internally on all parapodia but typically not emerging.

Posterior region becoming flattened, ending in small pygidium with two fragile terminal cirri. Last few setigerous segments without branchiae but with dorsal cirri and setae (reduced numbers). Maximum segment number about 200.

Material deposited in the Peabody Museum, Yale University, YPM No. 2695.

We have also examined forty individuals from the same population between 12 and 25 mm in length. The two smallest specimens (12 mm) show striking morphological deviations from larger members of the species (greater than 20–25 mm). Most striking is the enlarged condition of dorsolateral antennae (Fig. 4) and the very short condition of other occipital antennae. Many of the remaining small worms (12–25 mm) show a transitional condition for this character. Another interesting deviation found in the smallest worms is the absence of demarcation between the buccal segment and the first setiger. Two somewhat larger specimens of the forty examined had distinct prostomial pigment spots very much like those found on all specimens of *H. tubicola*. Comparing the morphological characters of these very small worms with those attributed by Ehlers (1887; see Fig. 6) to North American worms, we believe that he described as *Onuphis gracilis* an intermediate condition between juvenile and adult forms of *H. artifex* Verrill.

Hyalinoecia sp.

Finally, we have examined 50 specimens obtained by Dr. Gilbert Rowe at 33° 59′ N, 75° 46′ W. This station is very close to the

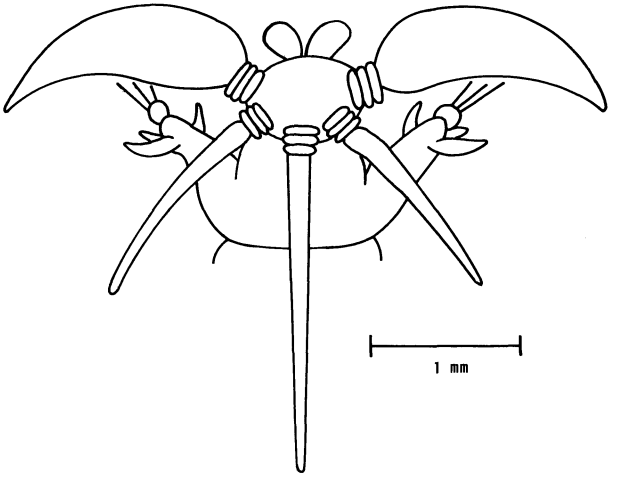

FIG. 4. *Hyalinoecia artifex* Verrill, continental slope (420–480 m). Anterior region of a worm 12 mm in total length, dorsal view.

previous one on the Atlantic continental slope, but at the considerably greater depth of 1125–1350 meters. The taxonomic status is particularly interesting because horizontal belts of quill worms are found at the two depths but not in between (Rowe, 1968).

DESCRIPTION OF MATERIAL COLLECTED. Prostomium bulbous, bearing five occipital antennae with annulate (3–4 rings) ceratophores, and two stout, short, frontal antennae without ceratophores. Three dorsomedial occipital antennae 3–4 times the length of the lateral pair. Unpaired median antenna extending as far as setiger XXVI; paired dorsomedial antennae extending as far as segment XIX. Single median antenna consistently longer. Prostomium without dark pigment spots. Ventrally two large globose palps forming the upper border of mouth.

Buccal segment dorsally forming an achaetous ring around base of prostomium. Mouth located ventrally with reniform lower lip and two protruding wing-shaped mandibles. Four pairs and one unpaired dark maxillae. Maxillae I hooked forceps. Right and left maxillae II with 12 (10–14) teeth. Right maxilla III absent; left with 8 (6–10) teeth. Right maxilla IV with 8 (6–13) teeth; left with 8 (6–11). Both right and left maxillae V without teeth, rudimentary.

Setigerous segment I very large, longer than succeeding segment. Parapodia enlarged, directed anteroventrally. Dorsal and ventral

cirri about same as on segment II. Presetal lobe fan-shaped (enlarged distally), covering bases of 2–4 stout, tapering acicula. Postsetal lobe small (one-half the size as on II), cirriform.

Setigerous segment II about two-thirds the length of I; parapodia smaller, more conical and directed ventrally. Dorsal and ventral cirri about the same size as on I. Presetal lobe somewhat spatulate covering bases of about 8 stout limbate and several pectinate setae. Postsetal lobe considerably larger than on I, more conical. Setiger III about three-fourths the length of II. Setiger IV about three-fourths the length of III, slightly larger than other body segments of the anterior and mid-regions.

Branchiae simple, flattened, beginning typically on setiger XX (XIX to XXII). Branchiae less than two-thirds width of body.

Limbate setae increasing to about 24 per fascicle in prebranchial segments. Emergent bidentate acicula appearing about setiger XXVIII, and increasing to two in posterior segments. Hooded acicula resembling those of *H. artifex*. Three stout, tapered, hooded acicula present internally on all parapodia but typically not emerging. Posterior region missing. Pectinate setae present in all but setiger I.

Material deposited in the Peabody Museum, Yale University, YPM No. 2696.

DISCUSSION

Shallow-water North American quill worms differ from their European relatives by the following morphological characters: 1) allometry of dorsomedial occipital antennae relative to lateral occipital antennae as well as to body segments; 2) allometry of median occipital antenna relative to paired dorsomedial antennae; 3) virtually complete absence of prostomial pigment spots; 4) adentate condition of acicula on anterior setigers; 5) morphology and smaller number of hooded bidentate acicula in branchial and mid-regions; 6) more posterior position of branchiae; 7) larger numbers of capillary and pectinate setae; 8) allometry of pygidium relative to body; 9) allometry of dorsal cirri relative to branchial filaments in mid-region.

North American worms differ from their European relatives by a number of other characters, the importance of which is difficult to assess. Some of these differences may arise from handling or

method of preservation; others, although undoubtedly natural, are of minor significance. The differences include: 1) allometry of frontal antennae; 2) disappearance of postsetal lobe on different setigers; 3) number of teeth on maxillae; 4) allometry of dorsal and ventral parapodial cirri on first and second setigerous segments; 5) larger mean size and segment number. It should be emphasized that these differences occur in worms of the *same overall size.*

The two North American populations also consistently differ from one another in: 1) number of limbate setae per fascicle; 2) allometry of occipital antennae relative to one another and to the body; 3) appearance of gills on different segments; and 4) rudimentary condition of maxillae V. While the absence of posterior ends prevents a quantitative size comparison, the lower slope specimens are approximately the same diameter. There are additional differences that we believe attributable to preservation of the lower slope specimens without prior removal from the tube. Because of the poor preservation and the absence of complete specimens from the greater depth, we do not consider our morphological comparison adequate. It is included here to call attention to possible morphological divergence correlated with the interesting ecological separation.

In conclusion, the differences between North American and European worms that were noted by Augener (1906) do exist; moreover, there are additional morphological differences. Contrary to the conclusion of Augener (1906), the differences are consistently found in worms of the same size. Since the synonomization is not supported by either evidence or well-founded argument, it seems reasonable to recognize Verrill's (1880) species *Hyalinoecia artifex* as distinct from the European form *H. tubicola* (O. F. Müller).

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