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A revision of the squid genera Corynomma, Megalocranchia, Sandalops, and Liguriella (Oegopsida, Cranchiidae)

by K.N. Nesis

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A revision of the squid genera Corynomma, Megalocranchia, Sandalops, and Liguriella (Oegopsida, Cranchiidae)

K. N. Nesis

Taxonomically, the Cranchiidae family is the most muddled of the squid families owing to the fact that many writers were describing new species and genera according to

the larvae and juveniles, often without even suspecting that they were not dealing with mature animals. But changes which take place during the cranchiids' growth are highly consequential, especially with regard to the very characters upon which the family's taxonomy was based (Chun, 1906; Pfeffer, 1912). As a result, larvae and adult forms of the same species ended up being classified as different genera and even different subfamilies. A particularly muddled system has been applied to the so-called Taonius — Desmoteuthis — Megalocranchia group, each of whose species has been frequently transferred from one genus to another in vain attempts to discover a "catch-all genus" (Pfeffer, 1912; Berry, 1912, 1916; Muus, 1956, 1962; Voss, 1960, 1963; Clarke, 1962, 1966; Adam, 1962; Roper et al., 1969; Zuev, Nesis, 1971). The genera Corynomma, Sandalops, and Liguriella are in a different situation: they have been described in their larval forms but have not as yet been allowed to "grow up" — with the result that their adult forms have not been identified among the many nominal cranchiid genera (Clarke, 1966). (5)

With a view to introducing some order into the cranchiid system of nomenclature one may either try to select a series of developmental stages of the same species and link the larval forms with the adults (Joubin, 1933; Muus, 1956), or reject as nomina dubia all names based upon the larvae and create a system based exclusively upon taxa related to adult

forms (Voss, 1967). (5)

Large collections of oceanic cephalopods, gathered during recent years by the research vessels "Vityaz'", "Akademik Kurchatov", and "Pyotr Lebedev", permitted an attempt to revise the chranchiid system through a selection of ontogenetic series. Unfortunately, in some cases it was necessary to employ a second, nihilistic method. The object of the present work is to provide new generic diagnoses grouped around Corynomma, Sandalops and Megalocranchia, to enumerate, and briefly — without redescription — to describe the species included in them, to provide a new, critically revised synonymy, and to present the horizontal and vertical distribution of the species involved. Basic information was collected by the Isaacs-Kidd midwater trawl method, mainly during the 50th expeditionary trip of the "Vityaz'" (1971), the 11th and 14th trips of the "Akademik Kurchatov" (1971-1973), the 1st, 2nd, and 4th trips of the "Pyotr Lebedev" (1961-1964). The author is indebted to N.V. Parin, V.M. Chuvasov, and Yu. G. Chindonova for the collection and relaying of data, to R. Kilias (Berlin), R. Young (Honolulu), M. Torkio (Milan), and M.R. Clark (Plymouth) for assistance in the work. The cranchiids from the collections made by the expeditionary vessel "Pyotr Lebedev" were preliminarily treated by G.P. Bulgakova, and I was able to take advantage of her valuable findings.

FAMILY CRANCHIIDAE

SUBFAMILY TAONIINAE

Corynomma Chun, 1906 (fig. 1)

Carynoteuthis Voss, 1960; Megalocranchia Pfeffer, 1884, pt.

G e n e r i c d i a g n o s i s. The mantle is cup- (or goblet-) shaped, rather narrow, of a membranous consistency, smooth, with a mucous cover. Posteriorly, the gladius is prolonged into a narrow, needle-shaped cone; the posterolateral edges of the lanceolate section (L. - lanceola) are concave. The fin is egg-shaped, with its halves anteriorly divided only by the lanceolate section (they do not extend to the lateral sides of the mantle); posteriorly, there is a needle-shaped "cercus" or caudal filament (fig. 1, *a*, *z*). The eyes are large and sessile (on short stalks in the larvae), with two photophores, the anterior one of which is club-shaped with a sharp curve on the external end (fig. 1, *u*). Two dumb-bell-shaped photophores with round lenses (in the adults) are located on the liver, on the ventral side of a large ink sac, and are visible through the mantle (fig. 1, *hc*). The median component of the funnel organ has two low triangular lobes, without a median papilla. There is a funnel valve (fig. 1, *3*). The arms have no photophores; they have highly developed protective membranes, no specially enlarged suckers, and the sucker disks are serrated. The tentacles do not autotomize; the club sucker disks on the distal end have sharp teeth.

(6)

Type-species: C. speculator Chun, 1906=Taonius abyssicola Goodrich, 1896.

Two species: Indo-Pacific C. a b y s s i c o l a (Goodrich, 1896) [C. speculator Chun, 1906 pt, 1910 pt; Megalocranchia maxima Sasaki, 1920, 1929 (non Pfeffer); ? Helicocranchia fisheri Berry, 1909] and the Atlantic C. o c e a n i c a (Voss, 1960) [C. speculator Chun, 1906, pt, 1910, pt, 1913; Megalocranchia abyssicola Joubin, 1924, non Goodrich; Carynoteuthis oceanica Voss, 1960; Phasmatopsis oceanica Clarke, 1962, 1966, Voss, 1963].

1(2). Rings (disks) of large club suckers distally with 10 - 12 large teeth, and proximally, with small teeth (fig. 1, *e*). Large arm suckers distally with closely adjacent turret-shaped teeth (fig. 1, *A*) . . . . C. a b y s s i c o l a

2(1). Disks of large club suckers distally with 6 - 8 large teeth; proximally — with small (fig. 1, *β*). Large arm suckers distally with low, rounded, irregular teeth (fig. 1, *б*) . . . . . C. o c e a n i c a

T A X O N O M I C O B S E R V A T I O N S. The type-species of the genus, C. speculator, is described on the basis of 3 specimens: 1 from the Indian Ocean (mantle length 11 mm), 2 from the Atlantic (11 and 32 mm); the holotype was not distinguished (Chun, 1910). The largest of them was obtained by the "Hauss" expedition, but during the survey of the cephalopods collected on this cruise (Thiele, 1921) no record was made,

with the result that even the geographical coordinates of the place where it was caught are unknown. Both of the small specimens were caught by the "Val'diviya". Since these belong to different species, I am selecting as the lectotype the specimen from the Indian Ocean ("Val'diviya", st. 237, 04°45′ S., 48°58′ E., catch 2000-0 m), as presented by Kun (1910, table 55, fig. 1-8). The type series is kept in the Natural History Museum at Berlin's Humboldt University (Museum für Naturkunde an der Humboldt-Universität zu Berlin). An analysis of the material from the "Vityaz'" collections shows that C. speculator is synonymized with Taonius abyssicola. The (8)
Atlantic species should be called C. oceanica. Voss (1960) conjectured that Carynoteuthis oceanica might prove to be the adult form of Corynomma. Megalocranchia maxima Sasaki (Japan) is obviously synonymized with C. abyssicola, as evidenced by the general appearance of the squid (Sasaki, 1929, table 25, figs.7-9), by the presence of photophores on the liver which, though not discernible, are painstakingly represented (table 25, fig. 8), by the funnel organ, arm suckers and tentacles. It is true that Sasaki records the absence of a funnel valve, but this valve is easy to overlook. It is not clear what is meant by the holotype Megalocranchia maxima Pfeffer, 1884 (South Africa; the specimen was not preserved): in outward appearance it is similar to Corynomma, but the optic photophore is not shaped like a club, but like a boomerang. It is necessary, therefore, to consider the designation M. maxima,

(cont'd .... p. 8)

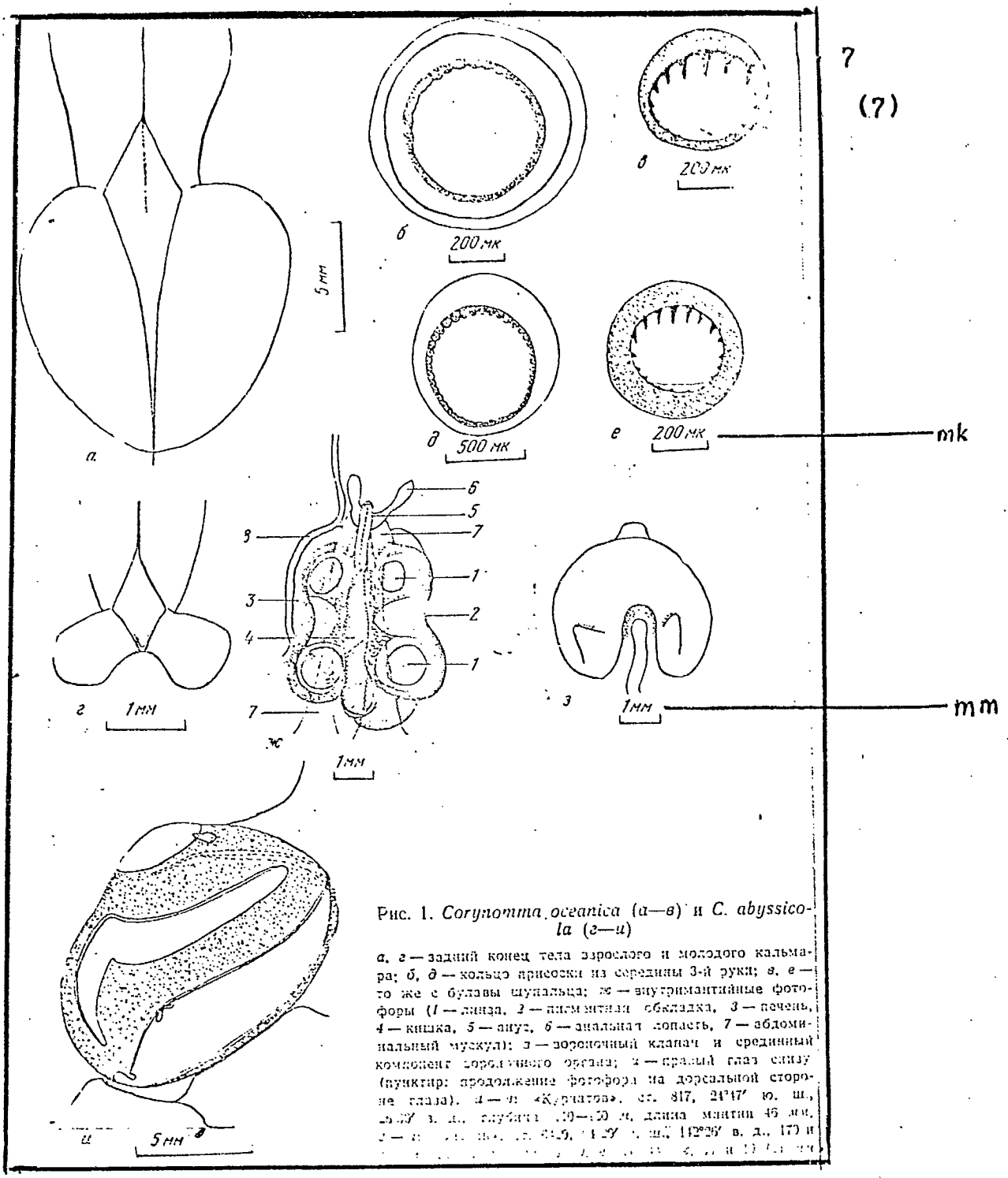

Рис. 1. *Corynomma oceanica* (*а—в*) и *C. abyssicola* (*г—и*)

а, г — задний конец тела взрослого и молодого кальмара; *б, д* — кольцо присоски из середины 3-й руки; *в, е* — то же с булавы щупальца; *ж* — внутримантийные фотофоры (*1* — линза, *2* — пигментная обкладка, *3* — печень, *4* — кишка, *5* — анус, *6* — анальная лопасть, *7* — абдоминальный мускул); *з* — воронковый клапан и срединный компонент воронкового органа; *и* — правый глаз снизу (пунктир: продолжение фотофора на дорсальной стороне глаза). *а—в*: «Курчатов», ст. 817, 24°47′ ю. ш., [illegible] з. д., глубина [illegible] м, длина мантии 46 мм, *г—и*: [illegible] ст. 6429, 4°29′ с. ш., 142°26′ в. д., 170 и

Fig. 1. Corynomma oceanica (*а-в*) and C. abyssicola (*г-и*)

а, г — posterior end of bodies of mature and young squids;
б, д — sucker disk from the middle of the 3rd arm;
в, е — sucker disk from the tentacular club;
ж — intramantle photophores (1 - lens, 2 - pigment lining, 3 - liver, 4 - intestine, 5 - anus, 6 - anal lobe, 7 - abdominal muscle; *з* - funnel valve and middle component of funnel organ;
и — view of right eye from below (dotted line: continuation of the photophore on the dorsal side of the eye).
а—в: "Kurchatov, st. 817, 24°47′S., 26°30′W., depth 110-150 m, mantle length 46 mm; *г—и*: "Vityaz'", st. 6429, 04°29′N., 142°26′E., 170 and 110m, mantle length 63 (*д,е,и*), 44 (*ж,з*) and 19 (*г*) mm

and, thus, the generic name based upon it, Megalocranchia, nomen dubium. Megalocranchia fisheri (Berry, 1909) (Hawaiian Islands) and Teuthowenia elongata Sasaki, 1929 (southern Japan), are probably also C. abyssicola. Other species included in the genus Megalocranchia will be considered below.

The genus Corynomma most closely approaches the genus Phasmatopsis with two species — Ph. cymoctypus Rochebrune and Ph. lucifer Voss, known up until now only on the basis of three mature females (Clarke, 1962; Voss, 1963). On the 14th cruise of the "Akademik Kurchatov" the young of both species were obtained for the first time, permitting a revision of the generic diagnosis. The young specimen Ph. cymoctypus was procured at 19°27′N., 67°51′W. in a catch at a level of 1500 m. The mantle length was 166 mm — twice as large as the largest of the known Corynomma; However, its sex has not yet been ascertained. The mantle's consistency is leathery, not jelly-like, like the mature Ph. cymoctypus. The fin is long and lanceolate, its length 43%, its width 13% of the mantle length; the anterior ends are joined to the mantle a little in front of the widest part of the lanceolate section. The buccal attachment is hepta-radial, the connectives are joined to the dorsal arms. The arms are long, with the largest being about 30% of the mantle length, strong, with extremely wide — larger than the thickness of the arms — protective membranes. 11 - 12 pairs of suckers on the 3rd arm are greatly enlarged, with a diameter up to 3.2 mm. These sucker disks have low rounded teeth around the whole

perimeter, the other suckers, —only on the distal end. On the distal parts of the arms we find the usual suckers with rounded teeth giving way abruptly to the typical small suckers with tusklike teeth. The tentacles are powerful, with clubs of the same structure as in Corynomma, but with a distinct carpal cluster of 10 suckers. The large club sucker disks have 10-12 sharp teeth on the distal end. As yet there are no photophores on the ends of the dorsal arms. On the liver there are two large dumbbell-shaped photophores with large lenses of exactly the same type as in Coryonmma. There is a funnel valve. The median component of the funnel organ has two large triangular lobes.

The difference between the young and mature specimens is very great and just the same as that which brings together the young of Ph. cymoctypus with the adults of Corynomma.

An immature Ph. lucifer female (mantle length 58 mm) was caught at night in the Caribbean Sea at $14^{\circ}43'$N., $73^{\circ}25'$W. at a level of 200 m. It differs from the holotype only in that the arm sucker disks on the distal end have even, high, rounded or blunt teeth, while the large club sucker disks have 6-8 sharp teeth.

Both species of the Phasmatopsis are significantly different than is usually the case in species of the same genus (Voss, 1963). In its bodily shape and fin structure, Ph. lucifer bears a resemblance to Egea inermis ;

(8)

this species is known only from an incompletely described holotype (Joubin, 1933; Roper et al, 1969), and until its redescription has been made, it appears impossible to solve the question of the unity of the species Phasmatopsis. (9)

H o r i z o n t a l and v e r t i c a l d i s t r i b u t i o n (see fig. 5). Both species are tropical. C. abyssicola is found throughout the Indian and Pacific Oceans. Its distribution in the Indian ocean is of the equatorial type, in the Pacific — of the equatorial-central western (Beklemishev, 1969). Localities where the species is found: between the Amirante Isles and Africa (Chun, 1910), around the Laccadive Islands (Goodrich, 1896), near the Osumi Is. (Sasaki, 1929), 0°00′ latitude 70°53′E.; 5°27′N., 80°07′E.; 0°58′S., 82°53′E.; 0°49′N., 87°07′E.; 8°30′S., 100°39′E.; 6°23′N., 135°36′E.; 13°31′N., 139°58′E.; 4°29′N., 142°26′E.; 2°36′S., 147°35′E.; 0°01′S. 175°56′W. (Vityaz' "); Sauqira Bay ("Skif"); 6°46′N., 95°22′W. ("Baikal"); perhaps also in Sagami Inlet (Sasaki, 1929), in the Kuroshio (Shevtsov, 1969) and in the vicinity of the Hawaiian Islands (Berry, 1909).

C. oceanica is found in the Atlantic, and its distribution consists chiefly of the bicentral type. Places where species is found: the northern subtropical regions from the Antilles and the Bermudas to the Azores and Canary Islands (Chun, 1910, 1913); Joubin, 1924; Voss, 1960; Clarke, 1969);

39°07′N., 58°09′W.; 20°43′N., 60°48′W.; 22°11′N., 66°33′W.(?); 23°08′ — 23°27′N., 66°53′ — 66°55′W. ("Pyotr Lebedev"); the northern part of the Caribbean Sea — over the Cayman trench and west of the Beata ridge ("Akademik Kurchatov"); the western part of the Mediterranean Sea (Joubin, 1924); the southern subtropical regions — South Equatorial Current (Chun, 1910); 24°27′S., 26°30′W.; 25°44′S., 26°38′W. ("Akademik Kurchatov").

Both species are mesobathypelagic; the young come up to the epipelagic zone. C. abyssicola is obtained in horizontal catches at depths of 50 - 500 m, and in total catches at depths of 530 - 2500 m, C. oceanica — in horizontal catches at depths of 100 - 1500 m, in total catches, at depths of 225-2500 m, and at the surface (larvae).

The most well-known specimen of C. abyssicola has a mantle length of 76 mm (Goodrich, 1896), C. oceanica — 80 mm (Joubin, 1924). In collections made by the "Vityaz'", "Akademik Kurchatov", and "Baikal", 84 specimens of C. abyssicola were found, with mantle lengths of 13 - 63 mm (in summer collections from the western part of the Pacific Ocean the majority of the specimens measure between 18 - 24, and 40 - 45 mm), and 14 specimens of C. oceanica with a mantle length of 12 - 63 mm. The animals were in schools, and in 1 catch, 10 - 20 specimens were obtained.

Verrilliteuthis Berry, 1916 (fig. 2, *a*, *б*)

Teuthowenia Chun, 1906, pt; Desmoteuthis Verrill, 1881, pt; Megalocranchia Pfeffer, 1884, pt; ? Ascoteuthis Berry, 1920.

(9)

G e n e r i c D i a g n o s i s. The mantle is goblet-shaped, fairly wide, of a membranous or leathery consistency, smooth, without a mucous cover. Posteriorly, the gladius is extended into a narrow, pointed, but not needle-shaped cone; the posterolateral margins of the lanceola are almost straight. The fin is an elongated oval, or lanceolate; anteriorly, both halves of the fin extend to the lateral sides of the mantle (in the adults); posteriorly, it is divided by the caudal filament and does not extend beyond it (fig. 2,a). The eyes are large, sessile (on short stalks in the larvae) with two or three photophores, the anterior one of which is crescent-shaped, not sharply curved. There are no photophores on the arms or the liver. The middle component of the funnel organ has three conical papillae. There is no funnel valve. The lateral pair of arms have several greatly enlarged suckers on the distal part, and their sucker disks (10) are smooth or slightly serrated. The tentacles do not autotomize, and the club sucker disks have sharp teeth along the whole perimeter.

Type-species: Desmoteuthis tenera Verrill, 1881=Owenia megalops Prosch, 1849= Leachia hyperborea Steenstrup, 1856.

Two species, one of them with two subspecies:
V. m e g a l o p s m e g a l o p s (Prosch, 1849) (Desmoteuthis hyperborea + Teuthowenia megalops Pfeffer, 1912; D. megalops + D. thori Degner, 1925; D. megalops Muus, 1956, 1962; D. pellucida Chun, 1913, non 1906, Grieg, 1922; Megalocranchia megalops Voss, 1960, 1967; Zuev, Nesis, 1971; Taonius megalops Clarke, 1962; T. megalops + Verrilliteuthis hyperborea Clarke, 1966) from the North Atlantic; V. m e g a l o p s a u s t r a l i s (Voss, 1967) (Megalocranchia megalops australis Voss) from the South Atlantic and the south-west part of the Indian Ocean; V. r i c h a r d s o n i

(Dell, 1959) (Megalocranchia richardsoni Dell) from (10)
New Zealand waters and the Tasman Sea.

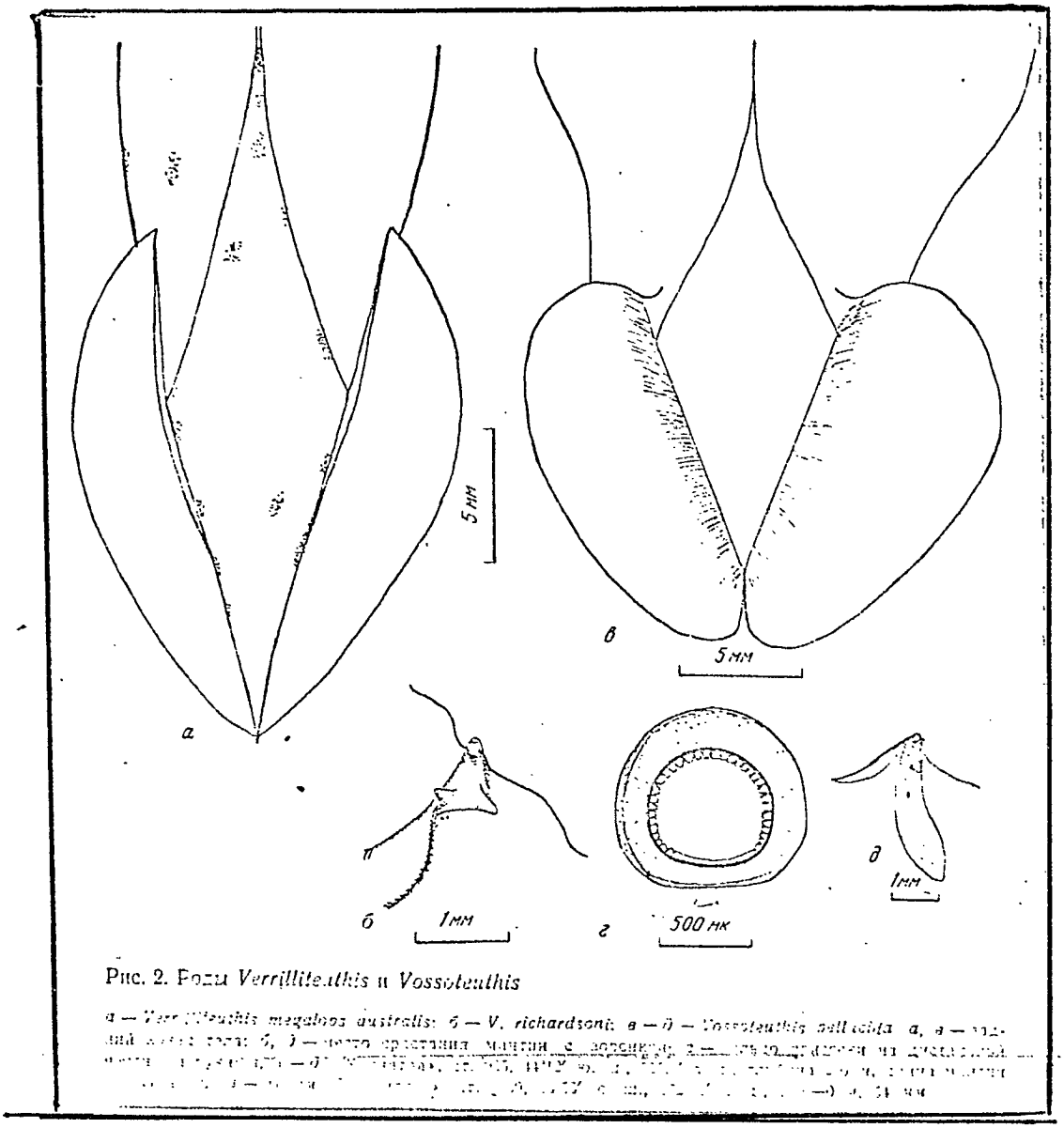

Рис. 2. Роды *Verrilliteuthis* и *Vossoteuthis*

а — Verrilliteuthis megalops australis; б — V. richardsoni; в — д — Vossoteuthis pellucida а, в — [illegible]

Fig. 2. Genera Verrilliteuthis and Vossoteuthis

а — Verrilliteuthis megalops australis; *б* — V. richardsoni; *в - д* — Vossoteuthis pellucida. *а*, *в* — posterior end of body; *б*, *д* — juncture of mantle and funnel; *г* — a sucker disk from the distal section of the 3rd arm; *а*, *в —д*: "Kurchatov" st. 935, 44°12′S., 55°20′W., depth of 230 m, mantle length — 76 (*а*) and 100 (*в-д*) mm; *б*: "Vityaz'", st. 3839, 36°53′S., 172°31′E., 1000—0 m, 54 mm

(11)

1(2). Each juncture of the mantle and funnel has one tiny conical cartilaginous tubercule. The fin length of the adults is 2/5 — 3/5 of the mantle length, the diameter of the eye is 10—15% of the mantle length . . . . . V. megalops megalops

2(1). Each juncture of the mantle and funnel (fig. 2,6) has 2 - 4 conical cartilaginous tubercles (in the very young, only one) 3

3(4). The fin length is 1/3 — 1/2 of the mantle length, the diameter of the eye approximately 20% of the mantle length . . . . . V. richardsoni

4(3). The fin length is approximately 1/5 —1/4 of the mantle length, the diameter of the eye is 10—15% of the mantle length . . . . . V. megalops australis

T A X O N O M I C O B S E R V A T I O N S. Owenia megalops is the oldest synonym of the type-species, and at the same time a type of the genus Teuthowenia Chun, 1910 (=Owenia Prosch, 1849, non delle Chiaje, 1844). Since this name is older than Verrilliteuthis, I should have used precisely that one. However, the holotype O. megalops is a larva, and the fact that this larva is, namely, Desmoteuthis tenera= Leachia hyperborea is true only inasmuch as in the Faeroes Islands (type locality of O. megalops) no other species of cranchiids are known whose larvae might be similar to O. megalops (Grimpe, 1933; Fraser, 1961; collections from the "Pyotr Lebedev"). If only two species of this sort were to be

found there, it would be impossible to ascertain to which adult form the O. megalops corresponds. For this reason, I prefer to base the generic name upon a species which has been described in its adult stage of development.

Several species have been confused under the name of Teuthowenia megalops: The Pacific Ocean "T. megalops" (Clarke, 1966; Okutani, 1969; Okutani, McGowan, 1969) are larvae of the Galiteuthis. "T. megalops" Joubin, 1933, possibly, is Vossoteuthis. An "anomalous form" of T. megalops from the equatorial Atlantic (Pfeffer, 1912)is probably an immature specimen of Helicocranchia pfefferi. From the detailed synonymy of V. megalops presented by Muus (1956), one must exclude Helicocranchia pfefferi, Teuthowenia antarctica and Desmoteuthis pellucida Chun, 1910.

Besides V. megalops, four more species were included in the genus Teuthowenia. Of these, T. antarctica Chun, 1910, is a larva of Galiteuthis glacialis (Chun, 1906)(=Crystalloteuthis glacialis), T. (Ascoteuthis) corona Berry, 1920, is most probably a young specimen of Verrilliteuthis (megalops)?; the T. elongata Sasaki, 1929, is perhaps a larva of Corynomma abyssicola, and the systematic position of T. tagoi Sasaki, 1929, is not clear, but it is obviously not Verrilliteuthis.

H o r i z o n t a l a n d v e r t i c a l d i s t r i b u t i o n (see fig. 5). The subspecies V. m. megalops is found in the North Atlantic, from the Sargasso Sea, the Antilles, the Canary

Islands and Cape Verde to south-west Greenland, the Strait (11)
of Denmark, the Faeroes-Iceland and Faeroes-Shetland ridges; it is recorded (with doubt) in the Caribbean Sea[1]; it is not found in the Norwegian, North, or Mediterranean Seas (Zuev, Nesis, 1971; Nesis, 1965; Clarke, 1966; Grimpe, 1933; Muus, 1956, 1962, Voss, 1955, 1960. A large specimen of V. m. megalops was caught near Angola (Adam, 1962), but it belongs, perhaps, to V. m. australis. The only authentic find of V. m. megalops in the equatorial Atlantic was made in the Gulf of Guinea ("Pyotr Lebedev", 2°35′ N., 3°48′ W., at a depth of 48 m, mantle length 26 mm). This squid is a common and numerous inhabitant of the northern-central and subarctic waters. Its base of distribution obviously lies in the northern-central waters and the subarctic circulation of the Irminger Current and southern part of the Labrador Sea, but in the Davis Strait and the Strait of Denmark, off the coast of West Africa (12)
south of the Canary current, and in the Caribbean Sea, there is a sterile zone of emigration.

V. m. australis is a subtropical-notal subspecies found in the south-west part of the Indian ocean, south-east of Natal, and south of Madagascar (Voss, 1967), and in the South Atlantic: 44°12′S., 55°20′W.; 44°02′S., 55°11′W.; 41°07′S., 26°21′W.; 41°10′S., 26°08′W.; 43°29′S., 26°17′W.; 43°20′S., 26°07′W. ("Akademik Kurchatov").

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[1]This squid was not found in the extensive collections of the "Akademik Kurchatov" from the Caribbean Sea.

V. richardsoni is known on the basis of five specimens caught at the eastern entrance to Cook Strait, and in Plenty Bay (Dell, 1959), as well as at 36°53′S., 172°31′E. ("Vityaz'"). Obviously, it is a south-subtropical species.

V. megalops is a mesobathypelagic species; the young live also in the epipelagic zone (Zuev, Nesis, 1971). In the "Pyotr Lebedev" collections, V. m. megalops were obtained in horizontal catches at depths from 48-50 up to 1400 - 1650 m. According to data of G. P. Bulgakova, the young of this subspecies make clearly defined daily vertical migrations, ascending around midnight to the epipelagic zone and dispersing during the day into waters at depths of 200-300 up to 1500 m. V. m. australis is found in horizontal catches and in the stomachs of lancetfish at depths of 80 - 960 m. In collections by the "Akademik Kurchatov" squid were caught at night and at dawn, at depths of 80-960 m; during the day — at 690-850 m. V. richardsoni was caught in total catches from depths of 457-1100 m, and in the stomachs of fish at a depth of 130 m. The largest V. m. megalops mantle length was 315 mm (Degner, 1925), V. m. australis — 89 mm (Voss, 1967), V. richardsoni — 130 mm (Dell, 1959).

The species of Verrilliteuthis are taken as samples in two forms — in limp (relaxed) condition or with contracted mantle muscles. The "limp" specimens have a transparent, relatively narrow mantle of a membranous consistency and a smooth surface; the "contracted" specimens — an opaque, very wide mantle, sharply

tapering into a thin tail, a membranous or leathery consistency and a surface covered with transverse wrinkles. The posterior ends of the "contracted" specimens are relatively longer (in relation to mantle length) than those of the "limp" specimens. These differences are apparently caused by biochemical processes in the mantle muscles at the time of the squid's death.

In nature, it is easy to identify squids of this type by their characteristic mottled colouration and a narrow, dark stripe in the mid-dorsum side of the mantle (Verrill, 1882; Dell, 1959; Voss, 1967).

V o s s o t e u t h i s Nesis, n. gen. (fig. 2, *Б–Д*)

Desmoteuthis, pt; Megalocranchia, pt.

G e n e r i c d i a g n o s i s. The mantle is goblet-shaped, with a membranous or leathery consistency, smooth, with a mucous cover. Posteriorly, the gladius terminates in a short, rhomboid lanceola and does not extend into a tail. The fin is rounded with both halves joined to the postero-lateral sides of the lanceola; anteriorly, these halves do not extend to the lateral sides of the mantle; posteriorly, they continue beyond the lower end of the gladius and either join, or remain separated by a narrow cleft (fig. 2, *Б*). The eyes are large, sessile, with two photophores, the anterior one of which is crescent-shaped. There are no photophores on the arms or on the liver. The median component of the funnel

organ has three conical papillae. There is no (12)
funnel valve. The lateral pair of arms have several greatly enlarged suckers on the distal section, with conical or turret-shaped teeth on the sucker disk rims (fig. 2,2). The tentacles do not autotomize, and the club sucker disks are toothed.

(13)

The grammatical gender is feminine. The genus was named in honour of G. L. Voss.

Type-species: Desmoteuthis pellucida Chun, 1910)

Two species: V. p e l l u c i d a (Chun, 1910) (Megalocranchia pellucida Pfeffer, 1912; Taonius pellucida Clarke, 1966. Non D. pellucida Chun, 1913, Grieg 1922), from the South Atlantic, and V. p a r d u s (Berry, 1916) Megalocranchia pardus) from the Tasman Sea and New Zealand waters.

1(2) Large club sucker disks with broad, low, blunt teeth. Each juncture of mantle and funnel has two small conical tubercles (fig. 2,∂) . . . . V. pellucida

2(1) Large club sucker disks with narrow, slightly blunted teeth around the whole perimeter. There are no (?) tubercles at the junctures of mantle and funnel . . . . . V. pardus

This key is tentative, since I did not see V. pardus, and the tentacular clubs were detached on my only sample/specimen of V. pellucida.

(13)

T A X O N O M I C A L O B S E R V A T I O N S. Squids mentioned without a description under the name D. pellucida and caught in the North Atlantic (Chun, 1913; Grieg, 1922), belong, in fact, to V. megalops megalops (Degner, 1925; Muus, 1956). The true V. pellucida may be easily distinguished from the V. megalops by the structure of the posterior end of the gladius, the fins. the arm suckers, etc. It is possible that the "Teuthowenia megalops" Joubin, 1933 from the North Atlantic belongs to the genus Vossoteuthis.

H o r i z o n t a l and V e r t i c a l D i s t r i b u t i o n (see Fig. 5). V. pellucida was found only twice: off South-West Africa (33°20′S., 15°58′E., catch at a depth of 1000-0 m; Chun, 1910), and at 44°12′S., 55°20′W., catch at a depth of 230 m ("Akademik Kurchatov"). It is apparently a subtropical-notal mesopelagic species. V. pardus was obtained at the Kermadec Islands (on the shore), near Wellington, New Zealand (on the surface), and (doubtfully) off South-East Australia and Tasmania (Berry, 1916; Dell, 1952; Allan, 1945). The south-subtropical species may be also mesopelagic. The largest known mantle length of the V. pellucida is 100 mm (our specimen), and that of V. pardus — 50 mm (Berry, 1916; Dell, 1959)

S a n d a l o p s Chun, 1906 (fig. 3)

Anomalocranchia Robson, 1924.

G e n e r i c d i a g n o s i s. The mantle is wide and goblet-shaped (wider than is usually the case with the Taoniinae),

of a leathery consistency, smooth, with a mucous cover. The gladius extends beyond the posterior end of the mantle and terminates in a broad, rhomboid lanceolate section — above, in the anterior half, it is flat; posteriorly, it is slightly roof-shaped, curved, with a weak longitudinal keel; the gladius does not extend into a tail-cone. The fins are kidney-shaped, are attached to the posterolateral sides of the lanceolate section, do not unite, do not extend to the lateral sides of the mantle nor reach the end of the gladius (fig. 3, а, б). The eyes are large and sessile (on long stalks in the larvae, with a bent rostrum), with two photophores, the anterior one of which is small, round or oval; the posterior one is very large (fig. 3, ж-и). There are no photophores on the arms or on the liver. The median component of the funnel organ has two broad triangular lobes and a small median papilla (fig. 3, в). There is no funnel valve. The arms are relatively very short, broad in the base sections, with wide protective membranes and small suckers; the sucker disks are almost smooth, with faintly visible low teeth (fig. 3, г, д). In the adults, the tentacles usually autotomize; distally, the club suckers are toothed (fig. 3, е).

Type-species: Sandalops melancholicus Chun, 1906 (= ? Anomalocranchia impennis Robson, 1924). The genus is monotypic.

T A X O N O M I C A L O B S E R V A T I O N S. In our data, all of the developmental stages of this species are represented. Its larvae are similar to S. melancholicus, but the adults resemble A. impennis. The larvae of Sandalops were found only a few

(cont'd ... p. 24)

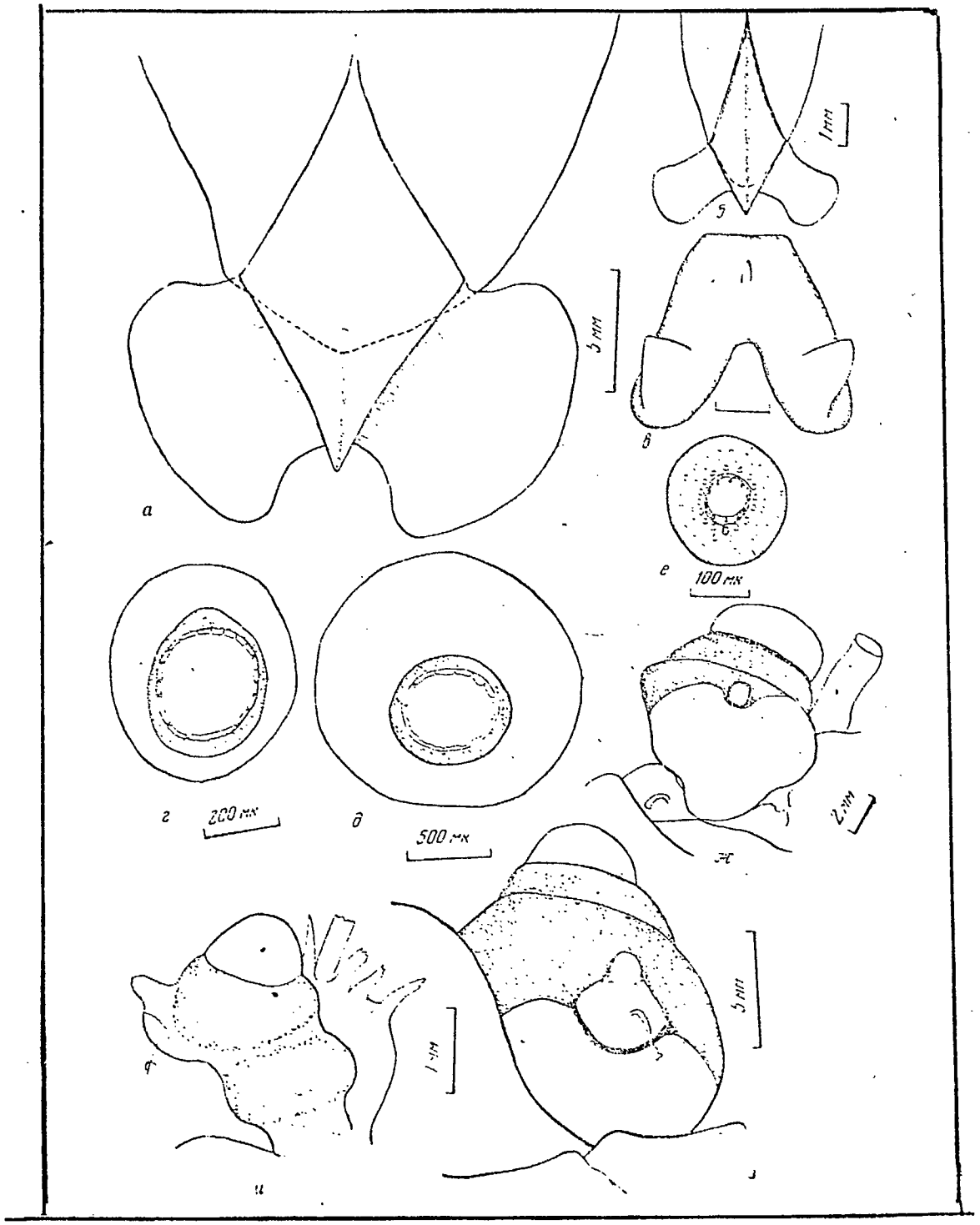

Fig. 3. (See legend on p. 23)

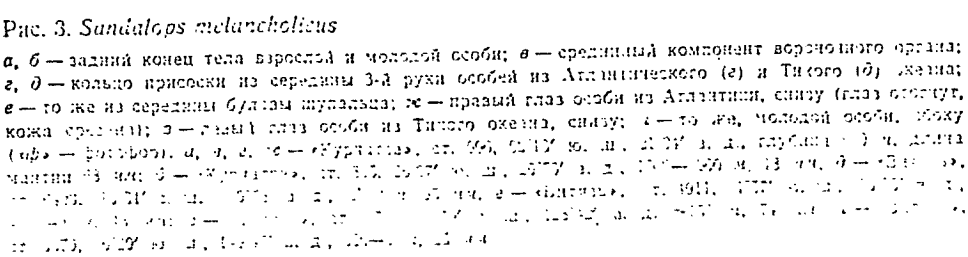

Рис. 3. *Sandalops melancholicus*

а, б — задний конец тела взрослой и молодой особи; *в* — срединный компонент воронкового органа; *г, д* — кольцо присоски из середины 3-й руки особей из Атлантического (*г*) и Тихого (*д*) океана; *е* — то же из середины булавы щупальца; *ж* — правый глаз особи из Атлантики, снизу (глаз отогнут, кожа срезана); *з* — левый глаз особи из Тихого океана, снизу; *и* — то же, молодой особи, сбоку (*ф* — фотофор). *а, з, и, ж* — «Курчатов», ст. 996, 02°13′ ю. ш., 21°04′ з. д., глубина — 600 м, длина мантии 68 мм; *б* — «Курчатов», ст. 835, 26°07′ ю. ш., 26°50′ з. д., [illegible] м, 18 мм, *д* — «Витязь», ст. 6493, 13°31′ с. ш., 139°58′ в. д., 1000 м, 95 мм, *е* — «Витязь», ст. 4911, 01°57′ ю. ш., 83°03′ в. д., 4500 — 0 м, 43 мм, *г* — «Витязь», ст. 3749, 19°59′ с. ш., 128°42′ в. д., ~150 м, 74 мм, *к* — «Витязь», ст. 3670, 06°29′ ю. ш., 149°45′ в. д., 500 — 0 м, 25 мм

Fig. 3 Sandalops melancholicus

а, б — posterior ends of adult and young specimens;

в — middle component of funnel organ;

г — sucker disk from the middle of the 3rd arm of an Atlantic specimen;

д — the same from a Pacific specimen;

е — the same from the middle of a tentacular club

ж — right eye of an Atlantic specimen, from below — (eye is turned back and skin is cut off); *з* — left eye of a Pacific Ocean specimen, view from below; *и* — the same of a young specimen, from the side ("*ф*" — photophore).

а, в, г, ж — "Kurchatov", st. 996, 02°13′S., 21°04′W., depth - 600 m, mantle length 68 mm; *б* — "Kurchatov", st. 835, 26°07′S., 26°50′W., 1500 - 1900 m, 18 mm; *д* — "Vityaz'", st. 6493, 13°31′N., 139°58′E., 1000 m, 95 mm; *е* — "Vityaz'", st. 4911, 01°57′S., 83°03′E., 4500 - 0 m, 43 mm; *з* — "Vityaz'", st. 3749, 19°59′N., 128°42′E., ~150 m, 74 mm; *и* — "Vityaz'", st. 3670, 06°29′S., 149°45′E., 500 - 0 m., 25 mm

(15)

times [Chun, 1910, and Thiele, 1921 (S. melancholicus, South Atlantic); Berry, 1920 (S. ecthambus and S. pathopsis, North-West Atlantic); Filippova, 1968 (S. melancholicus, Indian Ocean) Clarke, 1969 (Sandalops sp., North-East Atlantic); Shevtsov, 1969 (Sandalops sp., Kuroshio waters)] In a description of new species of Sandalops, Berry (1920) notes the possibility that both of them are merely stages of development of S. melancholicus. Apparently this is really the case. Clarke (1966) and Shevtsov (1969) do not give descriptions of their Sandalops; it is probably the same species.

The only known specimen of A. impennis, obtained near the Cape of Good Hope, is a severely contracted squid with completely detached fins. Some details of its structure (Robson, 1924 a,b) do not coincide with the features of our specimens; the club suckers have numerous teeth around the whole perimeter, and all three of the papillae of the middle component of the funnel organ are approximately the same. The meaning of these differences is so far unclear to me.

A comparison of Atlantic and Indo-West Pacific specimens from our collections did not enable us to detect any constant distinction between them; they are conspecific.

H o r i z o n t a l a n d V e r t i c a l D i s t r i b u t i o n. (see fig. 5). S. melancholicus is an Atlantic-Indo-West Pacific tropical mesobathypelagic species. In the Atlantic they are, for the most part, distributed bicentrally and are found in

the northern part of the ocean around the Bahamas (15) and Canary Islands (Berry, 1920; Clarke, 1969) and at the coordinates of 11°37′N., 63°12′W. ("Akademik Kurchatov"); in the southern part at 32°08′S., 8°28′W. (Chun, 1910; Thiele, 1921); at 2°13′S., 21°02′W. and along 26°30′W. from 24°30′ to 26°07′S. ("Akademik Kurchatov"); at 10°34′ — 10°46′ S., 26°09′ — 26°44′W. ("Pyotr Lebedev"); ? off South Africa (Robson, 1924). In the Indo-West Pacific, the species is distributed mainly in equatorial waters: 1°57′S., 83°03′E.; 18°26′N., 85°30′E.; 20°54′S., 113°08′E.; 19°59′N., 128°42′E.; 13°31′N., 139°58′E.; 4°29′N., 142°26′E.; 6°29′S., 149°45′E. ("Vityaz'"), and in the subtropical waters of the Kuroshio (Shevtsov, 1969). Squids were caught in the Atlantic in horizontal catches at depths of 150 - 1900 m, and in total catches at depths of 100 - 1100 m; squids larger than 35 mm were caught at depths of 600 - 850 m. In the Indo-West Pacific the squids were obtained in horizontal catches at depths of 110 — 1000 m, and in total catches from depths of 500 — 4500 m; specimens (16) larger than 35 mm were picked up at depths of 500 — 4500 m. There are ontogenetic vertical migrations; if there are daily migrations, they are not large. In our samplings from the Atlantic we found specimens with a mantle length of 9 - 68 mm, for the most part — 10-20 mm (18 out of 33 sp.), and from the Indo-West Pacific — 10 - 95 mm. The last specimen (caught at a level of 1000 m) was the largest known; not a trace of its tentacles remained, even the places of attachment were imperceptible, whereas in the larvae the tentacles are developed

and those of the "adolescents" usually autotomize; but in this case, the bases of the stalks were preserved.

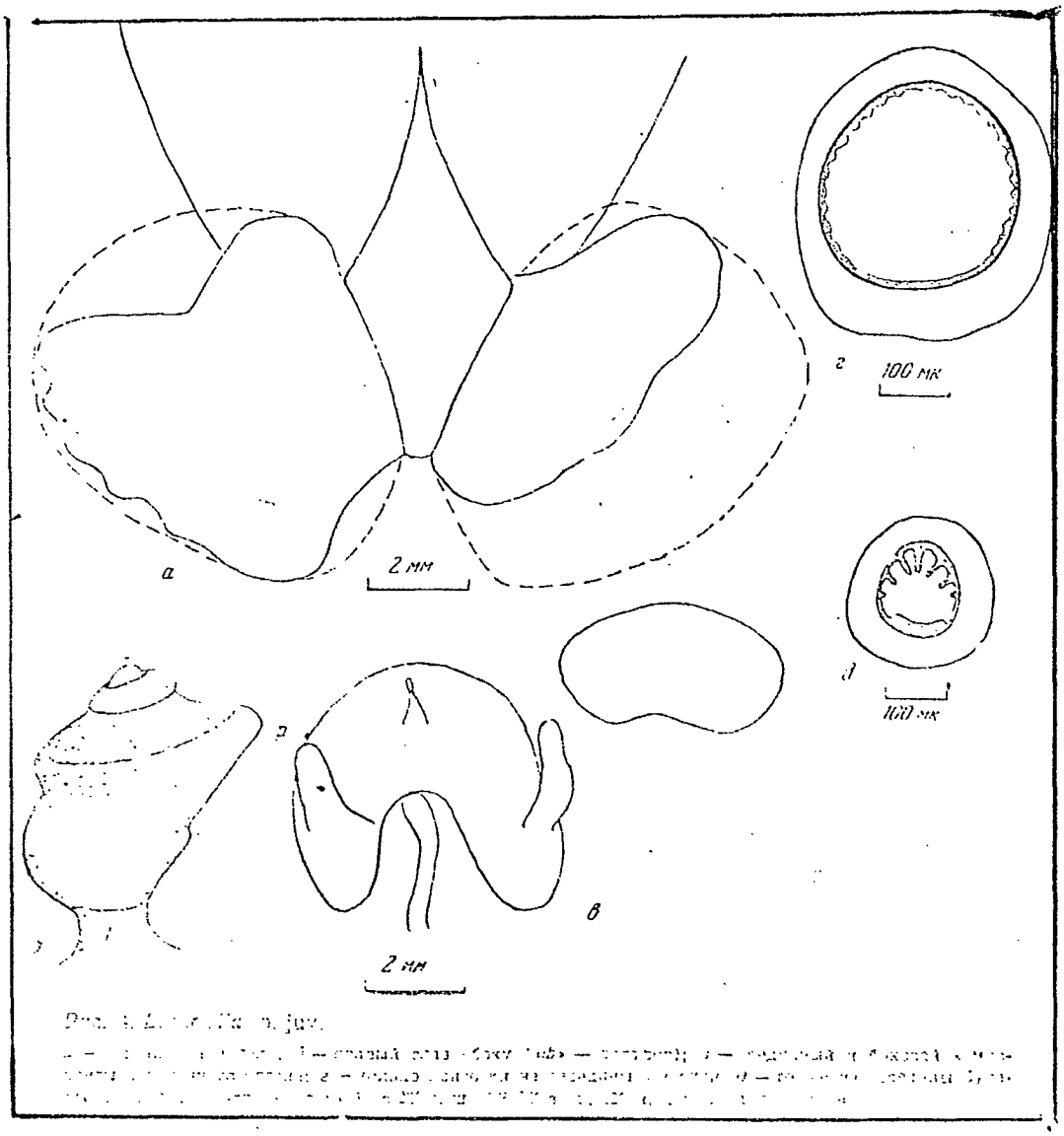

Fig. 4. Liguriella sp. juv.

а — posterior end of body; б — side view of right eye (("ф" — photophore); в — median and lateral components of the funnel organ; г — sucker disk from the middle of the 3rd arm; д — the same, from the middle of a tentacular club. "Vityaz'", st. 6469, 06°23′N., 136°36′E., 220 m, mantle length 52 mm

L i g u r i e l l a Issel, 1908 (fig. 4)

Bathothauma Allan, 1940, non Chun.

G e n e r i c d i a g n o s i s . The mantle is cylindrical, posteriorly rounded, of a leathery consistency, without a mucous cover. The gladius has a short lanceola, rhomboid or slightly drawn backward; the lanceola is not (17) hard, as it usually is, but soft, almost membranous; it does not determine the shape of the posterior end of the body which may extend beyond the gladius tip. The fins are short, oval, do not unite and do not extend to the lateral sides of the mantle (fig. 4, *a*). The eyes in the larvae are on short stalks (their structure in the adult specimens is not known), with two (?) photophores (fig. 4, *б*). The liver has no photophores. The middle component of the funnel organ has three papillae (fig. 4, *б*). There is no funnel valve. The arm suckers are toothed or serrated. The club suckers have some sharp teeth on the distal margin.

Type-species: Liguriella podophtalma* Issel, 1908. The numbers of this species are not established.

T A X O N O M I C A L O B S E R V A T I O N S. The only known specimen of L. podophtalma* — a larva with a mantle length of 9 mm — was obtained in the South-West Atlantic (Issel, 1908). Shortly after, the genus Liguriella was

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(Translator's note: * sic)

amalgamated with the synonym Corynomma (Chun, 1910) and subsequently reestablished (Pfeffer, 1912), but its systematic position remained obscure: It was connected at times with the subfamily Taoniinae (Chun, 1910), at other times, with the Cranchiinae (Issel, 1908; Pfeffer, 1912; Thiele, 1934). In materials of the "Vityaz'" there are 6 young squids (mantle length 17-52 mm) which undoubtedly belong to the Liguriella. A study of them established that the "saw-tooth tubercles" on the dorsal side of the mantle of the L. podophtalma* holotype (because of which the genus was associated with the Cranchiinae) were the result of numerous fractures in the gladius during the sharp contraction of the mantle at the time of fixation, while the group of "photophores" on the optic ganglion — clearly most unusual as a photophore location — is an artifact. Chun (1910) was right in not attaching much importance to these "features". Liguriella undoubtedly belongs to Taoniinae; its generic independence is clear from the diagnosis.

Our specimens are perhaps not conspecific with L. podophtalma*: the holotype's arm sucker disks are armed judging by the drawing (Issel, 1908, table 2, fig. 49) with widely spaced, pointed teeth along the whole perimeter; the club sucker disks have 4 sharp teeth, the two middle ones of which are much longer than the 2 outer ones (as in the Belonella larvae); distally, our specimens' arm sucker disks are very slightly serrated; proximally, they are smooth (fig. 4, 2); the club sucker disks have 3 long middle

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(* sic)

teeth with two short teeth on each side (fig. 4, ∂).

Also apparently belonging to the species Liguriella are the larvae (mantle length up to 13 mm) from the Australian waters, described under the name Bathothauma lyromma (Allan, 1940, 1945). Their difference from the real B. lyromma Chun was noted by Young (1970). In outward appearance they are similar to the smallest of our specimens; there was no detailed description of their structure. The Liguriella sp. from the California current (Okutani, McGowan, 1969) is obviously a larva of one of the "long-tailed" cranchiids.

D i s t r i b u t i o n. The species Liguriella (fig. 5) is found only in three widely-separated oceanic regions: in the Brazilian current (28°38′S., 47°32′W., catch at 600 - 0 m; Issel, 1908), in the Philippine Sea (6°23′N., 135°36′E., horizontal catches at depths of 200, 220 and 500 m), and off the east coast of Tasmania on the slope (Allan, 1940, 1945). This suggests that we are concerned here with three different species. The absence of mature specimens does not presently permit a solution to this problem. All three regions are to some degree subject to the influence of central waters, with the result that Liguriella may have a bicentral distribution. Thesesquids are probably mesopelagic or mesobathypelagic.

(18)

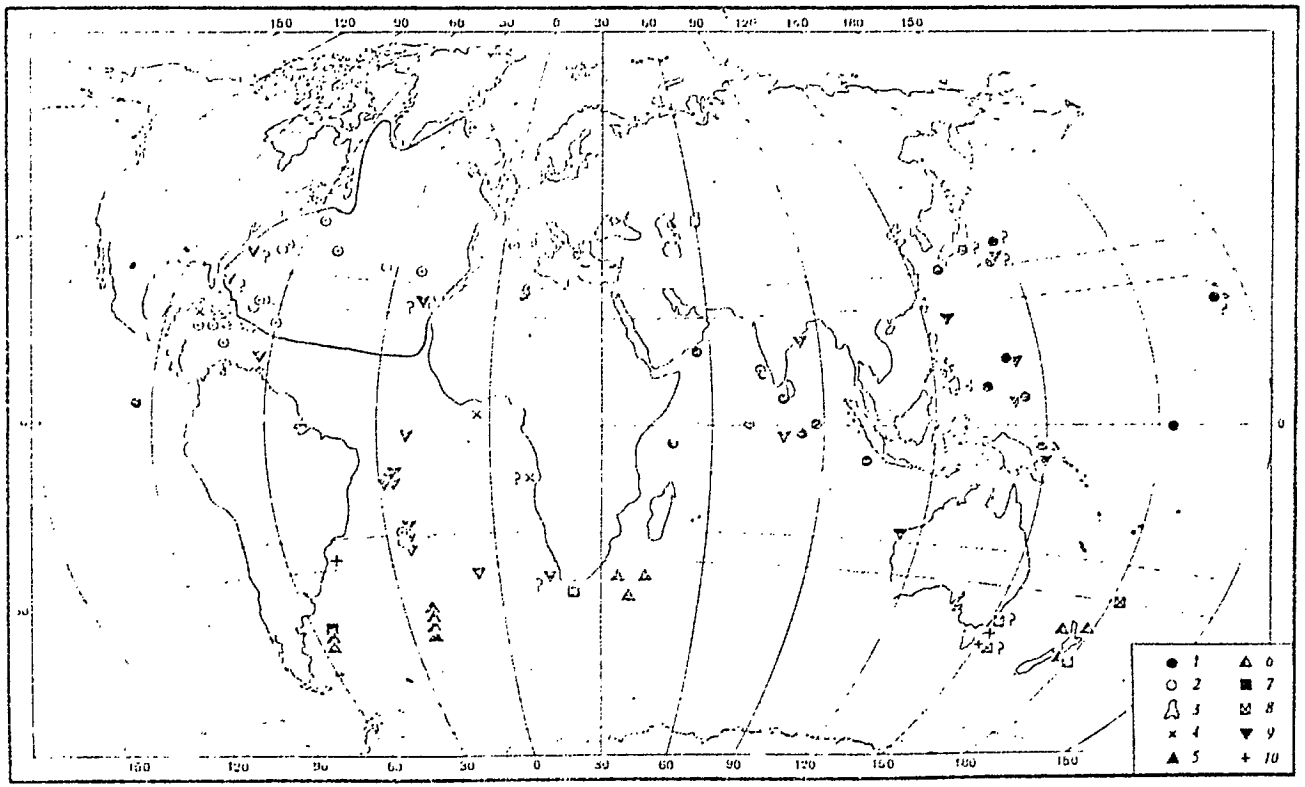

Рис. 5. Распространение видов *Corynomma, Verrilliteuthis, Vossoteuthis, Sandalops* и *Liguriella*

1 — C. abyssicola, 2 — C. oceanica, 3, 4 — V. megalops megalops (граница ареала и места отдельных находок за его пределами), *5 — V. m. australis, 6 — V. richardsoni, 7 — V. pellucida, 8 — V. pardus, 9 — S. melancholicus, 10 — L. podophthalma* и *L. sp.*

Fig. 5. Distribution of the species Corynomma, Verrilliteuthis, Vossoteuthis, Sandalops and Liguriella

1 — C. abyssicola, 2 — C. oceanica, 3, 4 — V. megalops megalops (boundary of its distribution and places of separate findings beyond these limits), 5 — V. m. australis, 6 — V. richardsoni, 7 — V. pellucida, 8 — V. pardus, 9 — S. melancholicus, 10 — L. podophthalma and L. sp.

DISCUSSION

The subfamily Taoniinae includes 14 quite comprehensively described genera: Taonius Steenstrup, 1881, Phasmatopsis Rochebrune, 1884, Belonella Lane, 1957, Galiteuthis Joubin, 1898, Mesonychoteuthis Robson, 1925, Corynomma, Verrilliteuthis, Vossoteuthis, Sandalops, Liguriella, Helicocranchia Massy, 1907, Ascocranchia Voss, 1962, Egea Joubin, 1933, Bathothauma Chun, 1906.

I consider the remaining nominal genera doubtful or invalid. Procalistes Lankester, 1884, Henseniоteuthis Pfeffer, 1900 (= ? Helicocranchia), Phasmatoteuthion Pfeffer, 1912, Fusocranchia Joubin, 1920, are known only through insufficiently described larvae; Leucocranchia Joubin, 1912 is a nomen nudum, Desmoteuthis Verrill, 1881 is synonymized with Taonius; Taonidium Pfeffer, 1900, Crystalloteuthis Chun, 1906, and Zygocranchia Hoyle, 1909 (Euzygaena Chun, 1910) are synonymized with Galiteuthis. Other names have already been mentioned.

The Taoniinae may be divided into four groups according to the structure of the terminal end of the gladius:

1. "Long-tailed" squids — the gladius is extended into a long sharp needle; the adults' mantle is of a gelatinous consistency — Taonius and Phasmatopsis; the mantle is of a leathery consistency and smooth — Belonella, Galiteuthis, Mesonychoteuthis.

2. "Medium-sized tail" squids — the gladius is extended into a sharp needle or narrow cone but is not as long as that of the preceding group: Corynomma, Verrilliteuthis.

3. "Short-tailed" squids — the gladius is not extended into a tail: Vossoteuthis, Sandalops, Helicocranchia, Ascocranchia.

4. "Tailless" squids — the lanceola is reduced: Bathothauma. Egea and Phasmatopsis lucifer constitute a kind of transition from the "long-tailed" to "short-tailed" squids, while Liguriella, with its membranous lanceslate section, forms a transition from the "short-tailed" to "tailless".

Each of these groups is compact and apparently homogeneous, but the resemblance between the genera included in the various groups is sufficiently great that this, together with the existence of transitional forms, makes it impossible to divide Taoniinae into taxa of a class higher than genus. The Taoniinae subfamily is a natural grouping.

Ontogenetically, most of the Taoniinae change most radically in the shape of the fin and structure of the eyes: The fin elongates acutely, the eyes shorten from stalked to sessile. In the most primitive types of Cranchiinae (Cranchia and Liocranchia) the shape of the fin and the structure of the eyes hardly change in ontogenesis. It may be assumed that among

the Taoniinae, also, the most primitive types are those in which the shape of the fin and the structure of the eyes have remained relatively constant during their course of development. This is characteristic of Helicocranchia, and possibly Ascocranchia if you compare it with Fusocranchia. Moreover, the structure of the optic photophores in the Ascocranchia is not typical of the Taoniinae but is similar to their structure in the Cranchiinae (Voss, 1962; Roper et al, 1969)[1].

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[1] A precise diagnosis of the species Ascocranchia based on analysis of a specimens of A. joubini taken from the tropical waters of the West Atlantic (19°33′N., 68°19′W., catch at a level of 1150 m, a young female, mantle length 64 mm, "Akademik Kurchatov" collections; goblet-shaped mantle, membranous consistency, in a mucous cover; a short lanceola, trowel-shaped fins attached to the lanceola on the posterior end of the mantle; vertical eyes with two-three small photophores on the anterior section (torn off in our specimen); no photophores on arms or liver; median component of the funnel organ with three conical papillae, no funnel valve; the third pair of arms were the longest; somewhat enlarged suckers on the middle sections of the lateral arms; arms' sucker disks with tiny teeth; third pair of arms in male hectocotylized; autotomizing tentacles; russet colouration with very small chromatophores.

Vossoteuthis and Verrilliteuthis diverged somewhat further from this original group. The other genera were obviously more specialized — it suffices to mention the gelatinous tissues of Taonius and Phasmatopsis, the shortening of the arms and autotomy of the tentacles in Taonius, Phasmatopsis and Sandalops, the development of hooks on the tentacles in Belonella, Galiteuthis and Mesonychoteuthis (as well as on the arms of the latter genus), the intramantle photophores of Phasmatopsis cymoctypus and Corynomma, the reduction of the lanceola and the extreme lengthening of the snout and eyestalks (in the larval stage) of Bathothauma.

If we analyze another characteristic — the structure of the middle component of the funnel organ — we arrive at a similar conclusion. The varied forms of this characteristic may be expressed in four types:
1) three finger-like or conical papillae, one median and two lateral; no funnel valve — Ascocranchia, Helicocranchia, Liguriella, Vossoteuthis, Verrilliteuthis, Belonella, Galiteuthis, Mesonychoteuthis; 2) two conical papillae, no median papilla or funnel valve — Bathothauma; 3) a finger-like or conical median papilla, lateral papillae converted into triangular lobes; no funnel valve — Sandalops, Taonius; 4) no median papilla, lateral papillae converted into triangular lobes; presence of funnel valve — Corynomma, Phasmatopsis. Egea's funnel organ is not described.

The first type is an initial one and reflects what might be called the basic branch of evolution (allomorphism) of Taoniinae: from the "short-tailed" forms with arm and tentacular suckers, to the "long-tailed", hook-bearing forms. The other three types correspond to various directions of specialization (telemorphosis).

The most primitive genera of Taoniinae, and also all the Cranchiinae, are tropical. Among the most advanced forms in evolutionary development are the subtropical and subtropical-boreal (= notal) — Verrilliteuthis, Vossoteuthis. Species which shun warm waters — the boreal, notal and antarctic species — represent only the most advanced genera of the basic evolutionary branch of the subfamily : Belonella, Galiteuthis and Mesonychoteuthis. That is, these squids differ from all of the other cranchiids in their exceptional mobility, activity, and elaborate adaptations for capturing large, mobile prey (hooks). The last member of this line, Mesonychoteuthis hamiltoni, is the largest species of cranchiid, indeed attaining gigantic proportions, and, at the same time, the most powerful and "fleshy". These three species appear to be an attempt on the part of the cranchiids to return again from the planktonic stage of life to the nectonic, that is, to return from the path of idioadaptation (idiogenesis) to the path of progressive development.

Other lines: Sandalops — Taonius, Corynomma — Phasmatopsis, Bathothauma, are lines of intensive specialization, adapted to

a purely planktonic form of life due to their "rejection" of active swimming and muscular tissues, long and powerful extremities, and the formation of supplementary photophores on the arms and the liver. In the most highly specialized forms of Cranchiinae, namely, in certain species of Leachia and Liocranchia, we find those same features: a gelatinous mantle, autotomy or weakening of the tentacles, and the emergence of intricately arranged photophores on the ends of the arms.

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A REVISION OF THE SQUID GENERA CORYNOMMA, MEGALOCRANCHIA, SANDALOPS, AND LIGURIELLA (OEGOPSIDA, CRANCHIIDAE)

Summary

Five squid genera are revised. The generic name *Megalocranchia* is admitted to be a nomen dubium and the species previously attributed to this genus are transferred to a new genus *Vossoteuthis* (type-species: *Desmoteuthis pellucida* Chun, 1910, non 1913), to *Verrilliteuthis* and to *Corynomma*. The name *Carynoteuthis* is synonymized with *Corynomma*, the name *Anomalocranchia* — with *Sandalops*. The independence of the genus *Liguriella* is confirmed. New diagnoses of all genera and the keys to the species are given. The data on horizontal and vertical distribution and maximal sizes of all species are presented. *Verrilliteuthis* consists of 2 spp. and 1 ssp., *Vossoteuthis* and *Corynomma* — of 2 spp. each, *Sandalops* — of 1, the composition of *Liguriella* remains unknown.

Evolutionary pathways in *Taoniinae* are analyzed. A comparative investigations of various systems of organs led to identical results. The main evolutionary line passes from *Ascocranchia* and *Helicocranchia* to *Galiteuthis* and *Mesonychoteuthis*. Most advanced genera of this line are more active and mobile and better adapted for preying upon active animals than other cranchiids, such process appears as an attempt to return from a planctonic mode of life to a nectonic one. The specialized evolutionary branches such as *Sandalops — Taonius, Corynomma — Phasmatopsis, Bathothauma* have lost activity and adapted to a purely planctonic mode of life. The most primitive genera are tropical inhabitants, among more advanced genera of the main evolutionary line there are some temperate and cold-water species.