Silurian aphrosalpingid sphinctozoans from Alaska and Russia

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The species of aphrosalpingid sphinctozoans earlier known from the Ludlow of the Middle Ural Mts of Russia, plus the new species *Aphrosalpinx nana*, *Nematosalpinx homathodes*, *Cystothalamiella alaskensis*, and *C. irregularis*, are described from the Ludlow part of the Heceta Formation of southeastern Alaska. This is the most diverse assemblage of Silurian sphinctozoans known. Only one other sphinctozoan species was previously recorded from the Silurian. *Aphrosalpinx textilis* and *Nematosalpinx dichotomica* occur also in other localities of the Silurian in southeastern, southwestern, west-central and south-central Alaska; the type specimens of these species from the Ural Mts are redescribed. The similarity of Silurian sphinctozoan assemblages from Russia and Alaska points out the strong paleobiogeographic relationship of the Nixon Fork terrane from west-central Alaska to the Alexander terrane of southeastern Alaska, and to the Ural Mts. Disjunct occurrences of several sponge species may also suggest ready access of marine faunas of northwestern North America and the Ural Mts region during the Silurian. The first recorded occurrences of a Ludlow orchoclad(?) sponge from southeastern Alaska are generically unidentifiable fragments from the Heceta Formation.

**Key words:** Porifera, sphinctozoans, systematics, Alaska, Silurian.

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Introduction

Sphinctozoan sponges are rare in the Silurian record. De Freitas (1987) described the only previously recognized Silurian sphinctozoan sponge, which was collected on Cornwallis Island in the Canadian Arctic. The major Middle Paleozoic gap in the sphinctozoan record was clearly shown by Senowbari-Daryan (1990: Text-figs 69 and 70), who cited the sponge described by de Freitas. Our paper adds several sphinctozoans to the Silurian record and documents the occurrence of those genera and species in the Silurian of southwestern, west-central, south-central, and southeastern Alaska, and the Ural Mountains of Russia (Fig. 1).

The present paper is based on collections made by Soja, collected in 1988-1993, and ones earlier collected by Blodgett (in 1979 and 1983), W.G. Gilbert (in 1979), A.T. Ovenshine (in 1967), B.L. Reed (in 1974), and C.L. Sainsbury (in 1959) from other localities in Alaska, and on Myagkova's type material. It now appears clear that Aphrosalpinx is restricted to Late Silurian strata in Alaska and Russia.

Figured and type materials are deposited in collections of the U.S. Geological Survey (USGS), the Field Museum, Chicago (FM), and in Department of Geology collections at Colgate University (BP, CP, MC, RP, SB, YP).

Taxonomic position of the aphrosalpingids

For many years Elizaveta Ivanovna Myagkova (1955a, b, 1960, 1984), Inessa Tikhonovna Zhuravleva (1960, 1970, and subsequent papers; also Zhuravleva & Myagkova 1970, 1971, 1972, 1974a, b, 1979, 1981, 1987) worked on a new group of fossils that they called aphrosalpingids, and which they included in their new kingdom of organisms, the Archaeata. Zhuravleva & Rezvoi (1956), in their comparisons of sphinctozoans (Thalamida) with archaeocyathids, claimed that sphinctozoans have many morphological characters in common with archaeocyathids. They listed a number of sponge and archaeocyathid genera that are very similar, and they included the Aphrosalpingoida in the sponge-archaeocyathid complex. Finks (1967) recognized the possible sphinctozoan nature of aphrosalpingids, with which we agree, and which, accordingly, we now also place among the sphinctozoans.

Myagkova (1955a, b), described and figured two new Ludlow aphrosalpingid families from the Urals, which she considered to be the youngest archaeocyathids. She placed them within a new class Aphrosalpingoida, with the two families included in two new orders, the Aphrosalpingiformes and Palaeoschadiformes, each of which was monotypic. Zhuravleva (1960) assigned the aphrosalpingids a taxonomic rank of subphylum, and placed them on the same taxonomic level as the subphylum Euarchaeocyatha within the phylum Archaeocyatha.

Vologdin & Myagkova (1962), in the Soviet Treatise on Paleontology (Основы Палеонтологии), included the class Aphrosalpingida within the phylum Archaeocyatha. They

Included in this class three orders: the Cambrian archaeocyathid Syringocnemida, and the Silurian Aphrosalpingida and Palaeoschadida. It was mainly this publication that influenced further Soviet work on the aphrosalpingids, and through translation made them known to non-Russian paleontologists.

In 1970 (and again in 1971 and 1972), Zhuravleva & Myagkova placed the Silurian Aphrosalpingida, together with Ordovician Soanitidae (North American calathids), Ordovician to Carboniferous Squamiferida (receptaculitids of non-Russian workers), and Cambrian archaeocyathids, in the new kingdom Archaeata. This kingdom of very primitive multicellular organisms represented a taxon undifferentiated into tissues or organs, with intercellular digestion and excretion, but without the differentiation characteristic of Eumetazoa. It appears that their definition of Eumetazoa differed from that accepted in the West. For discussion on the nature of Eumetazoa see Hyman (1940), who considered Eumetazoa as true Metazoa.

Zhuravleva (1970) in a theoretical paper, and later Zhuravleva & Myagkova (1979) argued that archaeocyathids evolved independently from other metazoans. Therefore, archaeocyathids could not have been included with sponges, but because of their 'multicamerality, skeletal microstructure, protuberances, (and) porosity' (Zhuravleva 1970: p. 55) concluded they were probably closer to protozoans. However, Zhuravleva & Myagkova at that time preferred to place archaeocyathids, because of their supposed multicellularity, together with the aphrosalpingids, receptaculitids, and 'other archaeocyathid forms' in a separate superdivision, Archaeozoa. They believed that sphinctozoans, although possibly close to sponges, were probably an independent group of a higher rank.

Zhuravleva & Myagkova (1974a: pp. 118–19, Pl. 16, Fig. 1) described the ecology of aphrosalpingids in bioherms, and figured Aphrosalpinx textilis in an algal-aphrosalpingid bioherm. These bioherms consist of blue-green algae and skeletons of tabulates, aphrosalpingids and other organisms. Aphrosalpingids occur as single individuals or as clusters, and are generally associated with algae. Zhuravleva & Myagkova (1981) also mentioned a 25-m long and 12-m high organic buildup composed of algae and aphrosalpingids in the Urals.
Zhuravleva & Myagkova (1981) strongly advocated placing aphrosalpingids within their kingdom Archaeata. By 1981 they had up to 600 specimens from the Urals and Salair (a mountain ridge in southern Siberia between the Ob and Tom rivers, extending along the northern border of the Altai Territory). These aphrosalpingids apparently existed during less than 10 Ma (million years), and are known from rocks of only one epoch (Ludlow). Although the aphrosalpingids were separated from the Euarchaeocyathids by some 120–150 Ma, Zhuravleva & Myagkova (1981) considered these two groups morphologically very close and, again, placed them together within the phylum Archaeocyatha.

The form and the diameters of the cups, the form of attachment (they introduced the term *radicatus* for the massive structures at the base of the cup serving for the attachment of the aphrosalpingids, sanomatids and euarchaeocyathids), and coloniality in these groups are different. Nevertheless, these organisms have a common structural plan of intervalium (*spongocoel*), presence of radial tubes (*siringa*, which they defined as locules in radial *internubes* in euarchaeocyathids and aphrosalpingids), presence of outgrowths (*exaules*) of the same type, and microscopic structures of the skeletons. The great morphological similarities of the genera *Aphrosalpinx* and the Early Cambrian *Syringocnema* Taylor 1910, and the placement of Aphrosalpingata within Euarchaeocyatha demanded that the ancestors of aphrosalpingids should be looked for among Syringocnematidae (Vologdin & Myagkova 1962). Thus, the range of that group of organisms was considered to be around 200 million years (Zhuravleva & Myagkova 1981: pp. 47–50).

Zhuravleva & Myagkova (1981: Pls 25–27) discussed the microscopic structures of the skeleton of *Aphrosalpinx textilis*, which was very similar to that of skeletons of euarchaeocyathids. The dimensions of the crystals were 5–7 μm, again within the range of the crystals of euarchaeocyathids. Well-developed cleavage and points of growth of new crystals were present on faces of crystals. The skeletons they examined were calcitic.

Myagkova (1984) summarized the Russian work on aphrosalpingids up to 1984. Zhuravleva & Myagkova, in their 1987 monograph, further argued for the validity of the placement of aphrosalpingids in the kingdom Archaeata, and they erected a new subphylum, Aphrosalpingata, which once more they described and illustrated in great detail. We observe here that, at that time, their taxonomic placement of aphrosalpingids was not as strange as it may now appear, because they combined archaeocyathids with sponges in what they called the kingdom Inferibionta, or primitive multicellular organisms. They placed that kingdom somewhere between the protists and animals, and suggested that it may have originated from the eukaryotes independently from all other eukaryotic kingdoms.

Hill (1965: p. 139), contrary to Zhuravleva & Myagkova (1981: p. 43), did not consider the aphrosalpingids to be algae. She only en passant questioned the sponge nature of the family Palaeoschadidae. It was Finks (1967) who first observed that 'If *Aphrosalpinx textilis* Myagkova, Sil Ludl, N. Urals (Myagkova 1955), should prove to be a guadalupiid sphinctozoan then this would be an earlier (st) record.' Finks considered the origin of the order Sphinctozoa as 'uncertain, perhaps from Archaeocyatha through *Aphrosalpinx* ' (p. 339). In 1970 he excluded Aphrosalpingoidea from the Calcarea *sensu stricto* (p. 14), and he pointed out in his chart (Finks 1970: Fig. 11 on p. 15) the relationship of aphrosalpingids with the sphinctozoans. He divided the sphinctozoan lineages into three stems — A, B, and C; part of Stem A could have been derived from *Archaeocyathus*?, and Stem C may have been derived from *Aphrosalpinx*?.

It is of interest that in the same volume as Finks (1970) and Zhuravleva (1970), Ziegler & Rietschel (1970) argued that the typical order Aphrosalpingida is closer to calcareous algae than to sponges or archaeocyathids. They based their conclusion on the similarity that they saw between the aphrosalpingids and some Paleozoic codiacean algae (e.g., *Palaeoporella*...
Stolley 1893). We are convinced that the relationship Ziegler & Rietschel (1970) saw between the aphrosalpingids and some Middle Paleozoic 'algae' is very real. However, we do not suggest that aphrosalpingids are dasyclad algae but that, instead, many so-called calcareous 'algae' may be sponges. We make this point now, for future discussion and work.

Hill (1972), in her revision of the Treatise on Invertebrate Paleontology volume on archaeocyathids, considered aphrosalpingids as an uncertain phylum of organisms, probably not archaeocyathids.

Nitecki & Debrenne (1979) acknowledged that they had opposed the union of various groups of Zhuravleva & Myagkova (1981), but nevertheless, they agreed that the unsatisfactory classification of these numerous taxa, reflected in the continuous reshuffling of the groups among sponges, algae, and other phyla, makes the creation of a single group for them a welcome relief. Therefore, if these forms could be shown to be related, then the concept of Archaeata should be accepted. However, Nitecki & Debrenne (1979) did not accept that the porosity or the presence of an intervalium, or even the existence of two walls, has been shown to be homologous. Therefore, they suggested that more information on the definition of a higher rank taxon, and, above all, on the biology of all these problematic groups is needed.

Nitecki & Fisher (1983), while having reservations about the rank accorded to the Archaeata by Zhuravleva & Myagkova (1981), strongly supported the relationships of some elements of the Archaeata, but suggested that the aphrosalpingids be removed from that complex, because they are sponges (Nitecki 1986).

It seems, however, that perhaps not all the criticisms against the ideas of Zhuravleva and Myagkova (see, for example, Zhuravlev & Nitecki 1985, Nitecki 1986, and references therein) were entirely warranted. When Myagkova described the aphrosalpingids in 1955, these forms were just discovered, and sphinctozoans were unknown from that early in the fossil record, therefore, it was not unreasonable to erect a new taxon for the reception of her taxa. Neither is the placement of archaeocyathids with sponges unreasonable. While we will not discuss the relationship of archaeocyathids to sponges, we point out that many workers are now returning the archaeocyathids to sponges (see, for example, Debrenne et al. 1990; Debrenne & Zhuravlev 1992; Zhuravlev 1989, and references therein). Furthermore, as seen in the most recent interpretation of the Burgess Shale (Gould 1989) questioning the permanency and early extinctions of some phyla is now acceptable. Unusual problematic fossils are turning up in many, though mostly Lower Paleozoic Lagerstätten. We have serious reservations about the validity of erection of new kingdoms of organisms based solely on fossils, and we are even more troubled by the removal of sponges from the animal kingdom; neither do we endorse many of the details of the Zhuravleva & Myagkova (1981) scheme of classification. Nevertheless, we must give them full credit for their pioneering work on aphrosalpingids, for describing and illustrating them, and for compar-
ing them with other fossil groups. We also feel that a detailed comparative analysis of all groups that Zhuravleva & Myagkova (1981) placed in Archaeata will have to be undertaken in the future.

Aphrosalpingids from Alaska

*Aphrosalpinx* was first reported in North America by Helen Duncan (in Sainsbury 1965) from the White Mountain area, McGrath A-4 quadrangle, west-central Alaska (Figs 1, 2B). These fossils were derived from an 'algal' limestone (USGS collection 5592-SD; =Sainsbury's field station, 59ASn16) from the lower part of Sainsbury's Dd unit (dolomite and limestone). The fossils came from rocks tentatively dated as Devonian(?) (Duncan in Sainsbury, 1965: p. C93). She based this assignment upon her uncertainty regarding the then current age determination of Russian *Aphrosalpinx* occurrences and about the stratigraphic significance of Uralian faunas then called Late Silurian in age. Another factor which influenced her was the co-occurrence with the Alaskan aphrosalpingids of a rugose coral identified by W.A. Oliver, jr. as close to Devonian *Leptoinophyllum*, but with the caveat from him that the material was 'inadequate for positive identification and a Silurian age cannot be ruled out' (Oliver in Sainsbury 1965: p. C93).

Blodgett (1983: p. 126) suggested a Lochkovian (early Early Devonian) age for the White Mountain aphrosalpingids, an age which he based on a sparse collection of co-occurring brachiopods. Subsequent larger brachiopod collections by Blodgett have convinced him that his earlier suggestion was in error, and that the aphrosalpingid-bearing strata of southwestern and west-central Alaska are Late Silurian (Ludlovian and/or Pridolian). Both Blodgett and W.G. Gilbert made sizeable collections of aphrosalpingids in the vicinity of White Mountain (McGrath A-4 and A-5 quadrangles, Fig. 2A-B) from the lower part of the S1 ('Silurian limestone') unit of Gilbert (1981).

The southwestern and west-central Alaskan aphrosalpingids are all from a Late Silurian 'algal' barrier reef complex which existed along the outer, seaward margin of the Nixon Fork terrane (Blodgett & Clough 1985; Blodgett & Gilbert 1992; Blodgett *et al.* 1984; Clough & Blodgett 1988). This barrier reef complex existed in southwestern Alaska during both Late Silurian and Early Devonian time, but aphrosalpingids have been recognized only from the Silurian part of the complex.

Aphrosalpingids have been recognized at only one locality (83RB40) in Nixon Fork terrane rocks outside the White Mountain area, in Upper Silurian 'algal' reef facies rocks exposed in the Taylor Mountains D-2 quadrangle in southwestern Alaska (locality 1 of Fig. 1; Fig. 2C).

An isolated occurrence of aphrosalpingids in rocks of uncertain terrane affinities in the Alaska Range of south-central Alaska (locality 3 of Fig. 1;
Fig. 2D) was collected by the late B.L. Reed, from his locality 74AR83 (=USGS 9721-SD), from the south side of Shellabarger Pass on the Talkeetna C-6 quadrangle. It is shown as locality 22 on the geologic map of the Talkeetna quadrangle of Reed & Nelson (1980) and occurs in their S1 ('Silurian limestone') unit, which consists of scattered, isolated exposures of massive, marbleized limestone. Rugose corals co-occur with aphrosalpingids at this locality, and were considered indicative of a Silurian or Devonian age (W.A. Oliver, jr., personal communication 1977). The only other age-definitive fossil collection from this unit, from their locality 25, yielded Silurian graptolites.

Ovenshine (Ovenshine & Webster 1970) was the first to discover specimens of what we now recognize as Aphrosalpinx in southeastern Alaska, which were discovered on Hoot Island, in the Sea Otter Sound area, west of Prince of Wales Island (locality 4 of Fig. 1; Fig. 2E).

Soja collected Aphrosalpinx and other sphinctozoans in southeastern Alaska (locality 4 of Fig. 1; Fig. 2E-G) from Ludlow beds in the Silurian Heceta Formation (Fig. 3). In the Alexander terrane, aphrosalpingids are associated with calcified microorganisms in three types of deposits:stromatolite reefs at the platform margin; quiet-water stromatolite mud mounds of shelf or slope origin; and slumps or debris flows containing stromatolite clasts that were transported downslope from the platform margin (Soja 1990; Soja 1991; Soja 1994). The aphrosalpingids are clearly restricted to the stromatolite buildsups and olistostromes and do not occur in shelf deposits, except as rare fragments, nor are they preserved in metazoan-dominated reefs at the platform margin. The sponges were highly integrated into the stromatolite boundstones, formed as much as 25 percent of the rock, and served as the nucleus of concentric, oncoid-like structures (Soja 1994).

In southeastern Alaska, the aphrosalpingids are associated with mainly microbial biotas. The stromatolite reef was built primarily by a Ludlowia association of 10 microbial taxa, as well as pentamerid brachiopods, encrusting bryozoans, and rare crinoid, stromatoporoid, and coral debris. The aphrosalpingids occur in stromatolite mud mounds with an Epiphyton-Sphaerina association that consists of six microbial taxa, as well as rare brachiopods and crinoids. A mixed assemblage composed of 10 microbial
taxa and fine-grained skeletal debris is associated with aphrosalpingids in debris flow and slump deposits. Details about associated biotas are in Riding & Soja (1993) and Soja & Riding (1993). Sponge-microbial relations, synecology, and paleobiogeographic implications of the Silurian stromatolites in southeastern Alaska were discussed by Soja (1994).


**Non-sphinctozoans sponges in Heceta Formation.** — Two sections of lithistid sponges occur in the collection (Fig. 14A–B). One shows regular network of dendroclones preserved as light-gray carbonate in medium-gray calcareous matrix. Individual dendroclones range from 0.2 to 0.3 mm long, with flared ends that appear to fuse to tips of other spicules to produce irregular coarse impressions of trabes, as seen in cross-sections. Some show flared divergent rays of spicule tips, from shafts approximately 0.02–0.04 mm in diameter and 0.2 mm long, but fabric is only crudely preserved and spicule identification is not possible. These spicule clusters define skeletal pores approximately 0.10–0.18 mm in diameter, now filled with somewhat darker crystalline calcite cement.

Other small fragment cut in thin section SB3-4EA2d-92 shows similar preservation but with suggestion that spicules are tricranoclones rather than dendroclones, in skeletal structure locally somewhat like Hindia. Skeletal net is so poorly preserved, however, that it is almost impossible to decide where sponge belongs taxonomically, beyond being a lithistid sponge. Triangular section is approximately 11 mm long and 7 mm wide, at maximum.

**Systematic Paleontology**

Class Demospongea Sollas 1875
Order Permospinhincta Termier & Termier 1974
Suborder Aporata Seilacher 1962
Family Aphrosalpingidae Myagkova 1955

**Emended diagnosis.** — Aporate sphinctozoans with deep spongocoel and surrounding chambers either glomerate or catenulate; steeply obconical to subcylindrical with single or branched stems. Central tube or spongocoel open or occupied by cluster of axial exhalant canals. Exaules, filling structures, and intertubes either present or absent.
Fig. 3. Generalized stratigraphic section of Silurian rocks exposed in the Sea Otter Sound area of southeastern Alaska (modified from Soja 1993). Arrows indicate sponge-bearing units.
Discussion. — The family Aphrosalpingidae was proposed by Myagkova, (1955a), and she and subsequent authors considered it as a family within the Archaeocyathida and, therefore, the initial descriptions were based on an archaeocyathid structural model. The Aphrosalpingidae (name derived from *Aphrosalpinx*) was proposed in early pages of the journal volume (Myagkova 1955a: p. 478), while the genus *Aphrosalpinx* was described later in the same volume, but in a separate paper (Myagkova 1955b). In the earlier description of the family, Myagkova included only a single genus, *Nematosalpinx*.

It appears that Myagkova originally wrote one paper, which was subsequently published in two parts (Myagkova 1955a, b). Myagkova was kind enough to provide us with a personal copy of her complete 1955 paper, in which, on p. 478, the original and first diagnosis of Aphrosalpingidae is corrected with an overprint reading Nematosalpingidae. She consistently followed this emendation in all her subsequent publications. Our translation of the 'original' diagnosis is from her 1955b paper.

What appears to be the same family, at least in its very generalized and broad-sweeping description, is the family Spicidae Termier & Termier 1977. Termier & Termier (1977: p. 38) established the new family Fistulispongidae, based on the Permian genus *Fistulispongia* from Djebel Tebaga. Their family included forms with a cellular chaetetid-like surface, but with mamelon-like chambers, each with an ostium, and all arranged around an axial structure. Senowbari-Daryan & Rigby (1988: pp. 200–201) observed that *Fistulispongia elegans* Termier & Termier 1977, is a *Spica spica* Termier & Termier 1977, overgrown by chaetetids and the family was clearly based on a genus synonomous with *Spica*. Fistulispongidae is thus a junior synonym of the Spicidae. Revised diagnosis of the Spicidae by Senowbari-Daryan (1990: pp. 118–119) is as follows: ‘in (this) family will be combined all aporate genera with a through-going spongo-coel. Arrangements of chambers catenulate or glomerate. Filling skeleton absent, with the exception of many species of *Vesicocaulis* and *Russospongia*. Based on glomerate or catenulate arrangement of segments, two subfamilies are differentiated: (a) Subfamily Spicinae [ ... ], glomerate arrangement of segments. (b) Subfamily Vesicocauliinae [ ... ], catenulate arrangement of segment’.

Senowbari-Daryan (1990: pp. 118–119) placed *Spica* Termier & Termier 1977, *Cystothalamiella* Rigby & Potter 1980, and *Uvacoelia* Kügel 1987, in the subfamily Spicinae. *Aphrosalpinx* Myagkova 1955, and *Nematosalpinx* Myagkova 1955 clearly should be included within the subfamily Spicinae as utilized by Senowbari-Daryan (1990). It is less certain whether *Palaeoschada* Myagkova 1955 should be included in this subfamily, although it may be. It is uncertain whether *Palaeoschada* is aporate, because of the existence of a solid inner layer of the chamber walls; in some specimens, however, the outer chamber walls clearly have pores. Other specimens in Myagkova's collection have walls with pores, but generally developed only in their outer parts. If *Palaeoschada* is included within the family, then all the Silurian sphinctozoans here described from Alaska belong within the family.
The family Aphrosalpingidae Myagkova 1955 has priority over the Spicidae Termier & Termier 1977 but the subfamily Spicinae Termier & Termier 1977 (transl. Senowbari-Daryan 1990), is a valid subdivision based on the genus Spica. In addition to the two subfamilies proposed by Senowbari-Daryan (1990), we are including within the family a third subfamily of somewhat questionable status — the Palaeoschadinae Myagkova 1955.

Genus *Aphrosalpinx* Myagkova 1955

Type species: *A. textilis* Myagkova 1955

*Aphrosalpinx textilis* Myagkova 1955

Figs 4B–G, J,K; 5A–E, G; 6; 8E; 11E–G; 12A, D, F.

*Aphrosalpinx textilis* sp. n.; Myagkova 1955b: pp. 640–641, Text-figs 1a–g, 2a–b.

*Aphrosalpinx textilis* Myagkova; Myagkova 1960: p. 89.

*Aphrosalpinx textilis* Myagkova; Vologdin & Myagkova 1962: p. 136, Figs 126a–d; Pl. 9', Figs 1–2.


*Aphrosalpinx textilis* Myagkova; Zhuravleva & Myagkova 1974a p. 119, Pl. 16', Figs 1–2.

*Aphrosalpinx textilis* Myagkova; Zhuravleva & Myagkova 1974b: Text-figs 1d, 2, 10, Pl. 1, Fig. 3.

*Aphrosalpinx textilis* Myagkova; Zhuravleva & Myagkova 1977, Pl. 7, Figs 1–4, Pl. 8, Figs 1–2, Text-figs 29a–b.

**Emended diagnosis.** — Steeply obconical, cylindrical, or goblet-like stems or branched, monogglomerate sponges with generally open axial spongocoel in middle and upper part, but with axial cluster of small exhalant tubes in lower part, canals ranging 0.15–0.25 mm in diameter. Sponges ranging from 4 mm to as much as 19 mm in diameter; spongocoels ranging from 1.5–2.0 mm across, in smaller branching stems, to 9–10 mm across in large obconical forms. Numerous chambers to approximately 1 mm high, radially arranged, with small endopores 0.15–0.2 mm in diameter, locally with S-shaped exhalant canals forming part of reticulate or vermiculate gastric layer intermediate between cortex-like lining in upper part and axial canal complex in lower part.

**Description.** — Two thin sections of Russian type material include moderately low-angle transverse sections and tangential sections. The best exposed specimen is a nearly complete section, approximately 14 mm in diameter, perforated by a central spongocoel approximately 6–7 mm across, although incomplete. Sponge walls monogglomerate, 3.5–4.0 mm thick, composed of honeycomb-like horizontal chambers, each 0.4–0.5 mm high, most of which are approximately 0.4 mm high at mid-height. Chambers gently upward arcuate, well-defined by imperforate or minutely perforate interwalls approximately 0.06 mm thick, composed of 2 or possibly 3 layers. Where 2 layered, upper layer is moderately organic-stained, darker, and somewhat finer crystalline than the light lower layer. Locally a thin, dark, lining occurs below the light layer in some chambers.
Walls composed of aragonite sphaerolites approximately 0.01–0.015 mm in diameter and rarely up to 0.02 mm across. Sphaerolites locally aligned, vertically, producing a pore-like structure, so that if walls porous, pores must be on a scale of the aligned sphaerolites.

Exopores in exowall, moderately large, 0.10–0.14 mm in diameter, and may be single, large, ostia-like opening that may be surrounded by thickened ring of wall or may extend a short distance as a tubular intertube to 0.2 mm into the outer chambers. Openings may extend as exhalates, up to 1 mm long, as irregularly curved tube, 0.18–0.20 mm in diameter. Vesicula may occur in the chambers but moderately rare.

Endopores lead to large upturned openings at inner ends of the chambers, and may be approximately 0.10–0.12 mm in diameter and up to 0.2 mm long, as neck-like openings or canals. These canals open into the vermiculate or vestibule-like openings between the endowall and the gastral screen-like structure, in the upper part of the sponge, or may open into irregularly curved exhalant canals, 0.10–0.15 mm in diameter, where the gastral layers thick, or where the entire axial exhalant area filled with a vermiculate, porous irregular complex. Latter complex developed in juvenile parts and where preserved in one specimen, for example, in

Fig. 4. Aphrosalpingid sponges from the Ludlow part of the Heceta Formation, Alaska. A. Nematosalpinx hormathodes sp. n., paratypes CP-3-89, transverse sections of two stems showing multiple exhalant canals in their axial clusters, surrounded by moderately cellular chambers in a single layer; x 3. B–G. J, K. Aphrosalpinx textilis Myagkova 1955. B, G. Specimen SB3-2E-89, vertical section through a fragment of the sponge wall, with the gastral surface on the left marked with prominent thin grid-like layer, vestibules connect to the open spongocoel through small pores, on the left; parts of short exhalates show as irregular small, circular extensions of the walls on the right in B; B, x 5; G, x 25. C. Longitudinal section through upper part of the cellular wall of a specimen from locality 8053-SD, showing upward-arched chambers with limited exhalates, on the right, and with a cortex-like screen along the gastral surface, on the left, as series of dark points produced by the grid-like structure; x 5. D. Specimen SB3-2E-89, vertical section through a fragment of the cylindrical upper wall showing the essentially horizontal chambers with a cortex-like grid forming the wall of the spongocoel, on the right, and the somewhat bubbly-appearing exhalates cut along the left; x 10. E. Specimen from USGS locality 5592-SD, tangential slice across inner ends of the chambers and the somewhat vermiculate-appearing lining of the spongocoel, in the transition area between where multiple exhalant canals are developed, below, and the grid-like gastral layer, above; small tube-like canals of this part of the exhalant system show in the upper left, in near-longitudinal view, but are cut across in the lower center; thick endowalls form dark skeletal rings in the lower center and thin interwalls show in the lower left and lower right; x 10. F. Specimen from USGS locality 5592-SD, somewhat diagonal transverse section produces false appearance of more than one layer of chambers in the sponge wall; chambers extend as prominent exhalates, on the right, from prominent ostia in the middle parts of the chamber exowalls (arrows); x 10. J. Specimen from USGS locality 8053-SD, somewhat diagonal transverse section of tubular chambers contain long intertubes or vesiculae, around an open spongocoel in the lower right, grid-like gastral layer shows as a series of dots separating the chamber wall from the open spongocoel; endopores of some chambers open into vestibule-like openings; x 5. K. Specimen CP3-89, somewhat diagonal, subtransverse section; x 5. A–I. Aphrosalpinx nana sp. n., diagonal sections on SB3-10EFL-89; both x 5. H. Holotype cut at a point of branching so lower chambers cut essentially trans-
versely, but upper chambers cut tangentially. I. Paratype, cut transversely in the lower part, but tangentially in the upper part.
section 7 mm in diameter is an axial complex 1.5 mm in diameter, completely filled with the porous vermiculate structure. Both pores and intervening irregular dark skeletal elements approximately 0.1 mm across or in diameter.

In upper areas where the central spongocoel is developed, the gastral lining may become somewhat vertically linear and attached to the endowall, forming a layer up to 0.7 mm thick, of linear tubelike openings as part of the gastral exhalant structure. In the upper part of the sponge, where diameters are large, only an irregular screen-like layer may occur, with elements up to 0.04 mm thick, separated by about the same distance, with pores through the screen-like structure. That screen may be separated from the inner part of the endowalls by up to 0.2 mm, in a vestibule-like structure.

Alaskan sponges, on the other hand, include steeply obconical to subcylindrical erect sphinctozoans with open axial spongocoel in upper part, as continuation above axial cluster of exhalant canals in basal part of sponge. Upward arcuate, broadly tubular, generally horizontal, radially and regularly arranged chambers are in single layer around spongocoel. Chambers may range from circular to scalariform in vertical cross-sections, and arranged diagonally in reference to those supra- and subjacent ones in uniform arrangements.

Diameters of spongocoel and axial cluster increase, for example, from only approximately 0.6 mm in sponges 2.5 mm across, to 1.4 mm in sponges 4 mm across, and to 2 mm across in sponges approximately 7 mm across. Axial canal cluster of circular to subprismatic vertical exhalant canals extend from near base of sponge up to where axial cluster reaches diameter of approximately 2 mm. Above that, exhalant canals form mesh-like reticulate, although vertically dominant, layer around gastral margin of spongocoel for few millimeters, but that layer reduced to porous grid or cortex-like layer in upper part of spongocoel margin, with remainder of spongocoel as open exhalant tube through upper part of sponge.

Exhalant openings in lower part of sponges extend from inner or gastral part of tubelike chambers as moderately small endopores, 0.10-0.15 mm in diameter. These pores empty into exhalant canals that flex up sharply to empty into the vertical exhalant canals in lower part of system, or into more vermicular upper part of excurrent system. Pores or canals 0.10-0.15 mm in diameter in latter area extend subparallel to margins of gastral surface in upper part of sponge, but diverge at moderately high angles to empty into open spongocoel in lower part of that opening. Such canals in lower part of sponges may be blocked by complete diaphragms across tubes. Diaphragms are spaced 0.5-0.7 mm apart in some of best developed tubes. suggesting that circulation in lower cells or chambers may have been limited, or that exhalant openings may have merged with those of other chambers and limited circulation through lower parts of the sponge.

Where the vermiculate gastral structure is best developed, as, for example, on thin section A-1, 2, USGS 5592-SD, these exhalant canals
are separated by moderately thick laminated elements, approximately 0.10 mm thick, as irregular discontinuous skeletal elements with dominantly vertical orientation. Elements may be discontinuous so laterally adjacent exhalant tubes may merge or become discontinuous where such canals cross-connect in moderately reticulate fashion in upper part of that filling.

In the lower part of the sponge, where reticulate filling is less defined, more continuous coarser exhalant canals form uniform reticulate net in interior of sponge as parallel axial cluster. These canals range from 0.15 to 0.25 mm in diameter, with older more central canals in middle part of cluster commonly with thicker walls and partially filled with laminated encrustations. Canals in outer rings are commonly separated only by thin dark micritic blades or walls, 0.02–0.03 mm thick. Similar dense walls are evident around each canal, but in more interior canals, a lining up to 0.06 mm thick partially fills the canals and produces circular canals from the dominantly subprismatic openings defined by dark primary canal walls. Such relationships are well shown on thin section CP-3-89.

In thin section 2947a, from USGS Locality 8053-SD, a longitudinal section through part of wall, exhalant canals exit through pores approximately 0.15–0.20 mm in diameter, and feed into S-shaped canals that rise steeply for approximately 0.5 mm from ends of chambers, but then flex sharply outward for approximately 0.5 mm, to exit through pores in the cortex layer, often with 2 or 3 pores in cortex layer per canal.

Sections not cut directly radially, parallel to individual tubes, may appear as though sponge is composed of double layer of chambers, but in best preserved material only single arcuate series of chambers consistently developed. Chambers range approximately 0.5–1.0 mm wide in upper coarser parts of sponge, but may be only half that size in smaller initial parts; chambers are approximately 0.5–0.8 mm wide through most of length of sponges. Chambers are approximately same height as width, ranging from approximately only 0.3 mm high in juvenile parts to as much as 0.6–0.8 mm high in upper more mature parts of sponges.

Chambers have strongly arched upper interwalls but may have moderately flat or planar lateral slopes. Walls may be relatively thin in middle parts of chambers but thicken both toward gastral and dermal surfaces in smooth intermediate parts. Planar parts may be only 0.02–0.03 mm thick, but flare slightly to thicknesses of perhaps 0.4–0.6 mm where merged with upper edges of subadjacent interwalls, at least in fossils from west-central Alaska. Specimens with chambers from southeastern Alaska are not as significantly scalariform, but have curved lateral slopes and crests producing spatulate sections. These chambers generally have walls approximately 0.04 mm thick, but range slightly thinner in central parts of chamber. Walls increase in thickness to as much as 0.1 mm near spongocoel margin, in zone where exhalant canals narrow, somewhat, before flexing up sharply into exhalant system.
Walls of chambers in best-preserved materials appear microlaminate and microcrystalline without major pores in even the best preserved material.

Chambers narrow and become almost cystose-appearing on exterior, but perforated in upper parts of ectowall of each chamber by a single large ostium, which commonly leads to prominent exaules. Ostia are generally 0.25–0.35 mm in diameter and continue distally as walled, single, tubular exaules of approximately same diameter. Exaules walls generally are 0.03–0.05 mm thick, with some irregularity. Exteriors of some exaules appear slightly nodular, but others are smooth tubular structures. Walls are essentially of same composition as interwalls between chambers in interior of sponge. Exaules extend radially and may be straight or slightly sinuous or irregular.

Some older parts have exaules blocked by vesiculae or diaphragms that are commonly arcuate outward, as thin impervious plates only 0.01–0.02 mm thick. Locally, these vesicular structures appear as continuations of laminar linings of exaules or of outer part of chamber walls. Such diaphragms generally occur in proximal parts of exaules tubes, commonly near chamber wall.

Fig. 5. Aphrosalpingid sponges from the Ludlow part of Heceta Formation of southeastern Alaska. A–E. *Aphrosalpinx* *textilis* Myagkova 1955. A. Specimen from USGS locality 5592-SD, transverse section showing the long cellular gastric layer of endotube exhalant canals on the lower and left side of the tubular spongocoel; prominent exaules extend radially from the exowalls of the chambers; × 3. B. Specimen from USGS locality 5592-SD, chambers cut tangentially give false impression of several layers of chambers around the spongocoel; prominent tube-like exaules show as distal extensions of exowalls on the left; × 3. C. Specimen from USGS locality 74AR83, vertical section of fragment showing tubular spongocoel and parallel walls composed of upward-arched chambers; × 3. D. Specimen RP-FL8 (-88), diagonal section showing radial chambers in the upper part where cut essentially parallel to their length, but more spatulate-appearing in the lower part, where cut tangentially; × 3. E. Specimen from USGS locality 9721-SD, transverse section showing radially arranged chambers; × 3. N. Tangential section of specimen YP58-3AFL-92, showing general spatulate to scale-like vertical cross-sections of the chambers. a few exaules show in cross-sections as circular, ring-like structures in chamber fillings; × 5. F. Specimen CP-3-89, lower transverse section shown in Fig. 4A; × 5. G. Specimen SB2-7.6EA6B-92, branched small sponge encrusted by microbial laminae; × 3. H. Specimen SB3-1WA-89, tangentially cut, globose, sections of chambers in the upper and lower parts of the sponge, and with part of the multi-tubular axial exhalant cluster in the central part (arrow); ostia to nipple-like short exaules and dark annular inner ends of ostia are cut in several chambers; × 5. J. Specimen SB2-4E-89, transverse section of large globose chambers in a single layer around a multichanneled exhalant canal cluster; × 5. K. Specimen SB3-4EA2b-92: steeply diagonal section showing globose chambers arranged in a single layer around a multi-tubed spongocoel, into which prominent endopores empty in the lower-center; vesiculae occur in several of the chambers; × 5. L. Specimen SB1-1WA-89, transverse section of three globose chambers, each with an exaulos, around a multiple-tubed, axial, exhalant cluster; × 10. M. Specimen SB3-4W-89, subtransverse section through a small spongocoel with irregular chambers arranged in a ring around a smooth, simple tubular spongocoel; × 10. N. Specimen SB1-FL12-89, small chambers with
mammiform-shaped exaules, section is tangential to the stem, in the upper part, and diagonally across a simple open tubular spongoecel into which a single endopore empties (arrow), in the lower center; × 10.
Fig. 6. Generalized reconstruction of Aphrosalpinx Myagkova 1955. Prominent tubular exaules extend from chambers. A tubular spongocoel has only a grid-like lining developed in the main upper part, but a more vermiculate, tubular complex lining the oval part of the opening, in that part of the sponge above where an axial cluster of small exhalant canals is well developed. Sponges are only a few centimeters in diameter.

In sponges approximately 3.5–4.0 mm in diameter, chamber layer is 1.2–1.5 mm thick and in sponges up to 8 mm in diameter, layer of chambers may be 2.5 mm thick, essentially the length of tubular chambers.

Vesiculae may be developed as filling structures within chambers, and are most common in lower or older parts of sponge as bubble-like or cyst-like plates, but many chambers appear to lack vesiculae or other filling structures. Inward extensions of exaules generally are only 0.25–0.3 mm long or less in dermal part of chambers, if present. Vesiculae are most common in specimens in thin sections from USGS Locality 8053-SD, where they appear almost like intertubes or inward extensions from exaules, but that cannot be demonstrated in material available. In some smaller early chambers, exaules extend as much as 0.5 mm into chambers, and may have bifurcated or branched tips or end as single openings in tubular structures.
Longitudinal vertical section of plate-like wall fragment occurs in thin section SB3-2E-89, and is approximately 10 mm long and 1.6–1.8 mm wide or thick. It consists of upward arcuate chambers, with an irregular, apparently knobby cyst-like surface on one side, but with a planar gastralt cortex on opposite side.

'Cortex' is thin, very porous plate approximately 0.1–0.2 mm thick, but locally as thin as 0.05 mm, that extends as porous sheet suspended approximately 0.08 mm out from gastralt surface. Skeletal elements are approximately 0.02–0.03 mm in diameter, separated by pores of essentially same dimensions, which communicate with irregular sub-'cortex' vestibule-like openings below. Vestibule-like canals approximately 0.04–0.05 mm in diameter connect to pores approximately 0.02–0.03 mm in diameter in reticulate 'cortex'. In the upper part, the 'cortex' appears more nearly solid, as though with some linear arrangement to pores, alternating with nonporous linear skeletal parts.

General form of species is well shown on samples from locality 83RB40 where numerous, multibranched stems, 4.5–6.0 mm in diameter, extend across sample. Nearly all stems are approximately 5.0 mm in diameter and branch somewhat irregularly in sponges at least 16 mm long or high. Stems are monoglomerate with single layer of favosus chambers arranged radially around central open spongocoel, 1.0–2.0 mm in diameter. Most stems have tubular spongocoel, 1.5 mm across, surrounded by walls 1.5–1.6 mm thick but ranging from 1.0–2.0 mm thick, and with chambers of that general length. Chambers are generally upward arcuate but may be almost horizontal and approximately 1.5 mm long, from moderately thick, only obscurely preserved endowalls, to outer ectowalls. Chambers are generally 0.3–0.4 mm high and occur 2–3 per mm, vertically, but 0.2–0.3 mm wide horizontally and 3 or 4 per mm measured parallel to circumference.

One somewhat larger specimen, associated with Nematosalpinx, on a sample from locality 83RB41, has diameter of 4.5–5.0 mm around central tube 0.7–0.8 mm in diameter. Chambers in walls are 1.6–1.7 mm long, producing walls around spongocoel slightly thicker than their length, and range from 0.5 to 0.7 mm high, with most approximately 0.6 mm high, but somewhat broader than height, ranging from 0.7 to 0.8 mm wide around circumference. Somewhat coarser chambers occur 1.5–2 per mm, vertically, and show somewhat coarser texture.

Upper part of large specimen occurs on sample from 79WG211; sponge is only moderately well-preserved, skeleton is 19 mm in diameter, with central open tubular spongocoel 9–10 mm in diameter. Walls are approximately 5 mm thick, of upward arched to nearly straight chambers, 0.3–0.5 mm high and wide, chambers with somewhat spatulate cross-sections. All of skeleton is preserved with moderately coarsely crystalline, recrystallized walls, but document occurrence of somewhat coarser sponges than materials in thin sections.
Material and occurrence. — Sections 1/39 (FM, PE39868), and 2/39 (FM, PE39867), from type collections of Myagkova, from Ludlow rocks, Vishera River, the Urals. Ludlow part of Heceta Formation in southeastern Alaska; species occurs on thin sections CP-3-89; RPFL-89; SB2-4E-89; SB2-FL2A-89; SB2-FL2C-89; SB3-2E-89; SB3-10EFL-89; YP58-3AFL-92; YP 58-4-89; and from locality 67AOv1422 (=USGS locality 8053-SD) on Hoot Island; and from ‘algal’ limestone in the White Mountain area, McGrath A-4 and A-5 quadrangles, west-central Alaska, at USGS locality 5592-SD; and localities 79WG18, 79WG170, 79WG211, 83RB4 and 83RB42; from equivalent ‘algal’ limestone in the Taylor Mountains D-2 quadrangle southwestern Alaska at locality 83RB40; as well as from ‘algal’ limestone exposed on the south side of Shellabarger Pass in the Talkeetna C-6 quadrangle, south-central Alaska, at USGS Locality 9721-SD (74AR83).

*Aphrosalpinx nana* sp. n.

Figs 4H-I, 5M-N, 12B.

Holotype: Thin section SB3-1EFL-89; Fig. 4H.

Type horizon and locality: Ludlow part of Heceta Formation; Prince of Wales Island, northwest of Twin Mountain, locality SB3.

Etymology: *Nana*, Latin, dwarf, in reference to the small size of the sponge.

Diagnosis. — Small cylindrical to steeply obconical stems up to 2 mm in diameter, monoglomerate chamber layer around axial spongocoel to 0.4 mm in diameter. Chambers approximately 0.2 mm high. Short exaules approximately 0.05 mm in diameter producing mammiform globose chambers. Endopores small, to 0.04 mm in diameter, with or without endotubes. Thin-walled canal tubes 0.05 mm in diameter, when present in reticulate gastral lining of spongocoel.

Description. — Cylindrical to steeply obconical stems may have axial canal cluster in lower parts but open spongocoel above, around which are arranged radiating tubular chambers in single layer. Adult stems are 1–2 mm in diameter, with walls up to approximately 0.5 mm thick around simple axial spongocoel, 0.3–0.4 mm in diameter in adult stages, but smaller in initial stages of sponge where simple axial spongocoel may be only 0.1–0.2 mm in diameter. Lower spongocoel is surrounded by ring of five or six globular chambers, but chambers become more distinctly tubular radially upward in sponge.

Initial chambers may be somewhat mammiform, where single exaules extend nipplelike to 0.1 mm out from arched sponge wall in middle part of exowall. In more mature parts, chambers are approximately 0.16–0.22 mm high, in a layer approximately 0.7 mm thick around an axial spongocoel, which is 1.4 mm in diameter.

Chambers are connected to the tubular spongocoel by small endopores, 0.03–0.04 mm in diameter, as direct openings without tubes. In upper, more complex, parts of skeletons, endopores empty into small, thin-walled canals, approximately 0.05 mm in diameter, that extend upward along
chamber walls for as much as 0.4 mm before emptying through the reticulate structure into the simple open tubular spongocoel. Chambers may share tubular openings. Ostia of exaules are 0.05–0.06 mm in diameter, and with thin walls approximately 0.01 mm thick where seen in juvenile parts of sponge, where all chamber walls are approximately 0.03–0.04 mm thick. Chambers are diagonally spaced and appear subspherical to spatulate, or scalariform in tangential sections. Vesiculae are not evident in small chambers.

Transverse section of initial part of small sponge shows axial spongocoel approximately 0.2 mm in diameter, with 3, radially arranged, globose chambers, from which extend irregularly curved exaules. Chambers are approximately 0.2–0.3 mm across, with ectopores 0.1 mm across. Exaules up to 0.15 mm across extend up to 0.25 mm out from ectowalls as definitely curved structures.

Associated somewhat larger specimen has axial spongocoel 0.15 mm across and 6 chambers arranged in a ring around it, cut only in partial sections. These occur inside another ring of 10 chambers that also are only partially preserved because of their globular appearance. Mammiform exaules, approximately 0.1 mm in diameter, extend out from them, as seen on thin section SB1-10-89.

Isolated tangential and moderately high-angled transverse sections occur in several other sections, including one on section SB3-4W-89, in which spongocoel is approximately 0.2 mm in diameter and layer of chambers approximately 0.4 mm thick. Chambers definitely are more elongate and cellular or tubular rather than globose, but with same generally curved to mammiform exaules from ectowalls of the tiny chambers.

Discussion. — *A. nana* is characterized by its small size, with adult chambers less than half the size of those in *A. textilis* Myagkova 1955. It may be of the same stem diameter as the branching *Nematosalpinx hormathodes* sp. n., but that species has an axial cluster of long continuous axial canals and has globose chambers throughout its extent. This small species does not have the favosid wall developed as well as in *A. textilis*. The tubular open spongocoel is much like the upper part of a complete *A. textilis*, but is several times smaller. These small sponges have the same dense microcrystalline skeletal structure seen in most of the other associated sponges and lack the porous outer walls characteristic of *Palaeoschada crassimuralis* Myagkova 1955.

Material and occurrence. — Holotype and paratype on thin section SB3-10EFL-89; and paratypes on thin sections MC-8A3-89, SB1-10-89, SB1-FL12-89, SB3-1WA-89, SE3-4W-89, YP58-2FL-92, YP58-4-89; Heceta Formation, southeastern Alaska. The species also occurs as a reference specimen on FM PE39867 from Myagkova’s collection from Silurian rocks on the Vishera River, the Urals; and somewhat questionably at Locality 83RB40 in the Taylor Mountains D-2 quadrangle of southwestern Alaska.
Genus *Nematosalpinx* Myagkova 1955

Type species: *Nematosalpinx dichotomica* Myagkova 1955.

**Diagnosis.** — Cup cylindrical dichotomously branched. Diameter 3–5 mm, intravallum consisting of radially arranged short tubular loculi, with diameter 0.2–0.3 mm. Inner cavity slightly larger than 1/3 of diameter of cup. Filled with skeletal tissue pierced by longitudinal canals, pointing exteriorly and communicating with loculi. Canals with multilayered calcified walls arranged longitudinally. Vesicular tissue of very thin membrane rarely observed in tubular loculi and longitudinal canals of central cavity. Membrane thickness 0.07–0.15 mm; attachment and propagation unknown (translated from Myagkova 1955a: p. 478).

*Nematosalpinx dichotomica* Myagkova 1955

Figs 11A–B; 12C–E.

*Nematosalpinx dichotomica* sp. n.; Myagkova 1955a: p. 479, Fig. 1.

*Nematosalpinx dichotomica* Myagkova; Vologdin & Myagkova 1962: p. 136, Pl. 9, Text-figs 3–7, Fig. 127a–d.


*Nematosalpinx dichotomica* Myagkova; Zhuravleva & Myagkova 1987: p. 54, Text-fig. 29B.

**Emended diagnosis.** — Branched monoglomerate sponges with stem diameters to approximately 5 mm, with globose to cellular chambers in single layer around a continuous axial cluster of exhalant canals, clusters to 2 mm in diameter, composed of numerous small canals, 0.2–0.3 mm in diameter. Chambers upward arcuate to cellular, to 1.4 mm long, horizontally, to 3 mm wide and 4 mm high, in crudely, hexagonal spacing. Single, large endopore per chamber, exaules obscure if present.

**Description.** — In a thin section of Russian type material, 7 or 8 cylindrical to branched, ramose sponges occur; one with three branches, one with at least two branches and several others that are transverse or high angle longitudinal sections to cylindrical sections of stems. Stems range 2.2–2.5 mm in diameter, with most approximately 2.5 mm across. Longest section is steep, sub-longitudinal section, 11 mm long, of a curved stem. Stems monoglomerate, with single layer of honeycomb-like chambers around an axial cluster of exhalant canals.

Axial clusters range 0.7–0.8 mm in diameter, and include up to 20 or 30 canals per cluster. One cross-section, approximately 1 mm in diameter, with 23 thick walled canals 0.10–0.13 mm in diameter, with most approximately 0.11 mm in diameter. They are upward extensions from endopores, approximately 0.06–0.08 mm in diameter, that lead from inner ends of chambers, through short canals, up to 0.10 mm long, then bend sharply upward to merge with the vertical exhalant canals of the clusters. Canal walls, dense, darker than the somewhat sparry-appearing interwalls and exowalls of the chambers. Canal walls 0.02–0.03 mm thick, where canals are side-by-side, but range up to 0.08 mm across in areas between trianguarly, or quadrangularly-spaced canals, in somewhat moderate
loose packing. Canals are vertical and cylindrical, with circular cross-sections and canal walls appear to lack pores and be composed of dark, organic-rich, micritic, dusty-appearing carbonate.

Monoglomerate chamber layer around exterior of the stem, 0.8–1.1 mm thick, of essentially horizontal favosus chambers, with spatulate to arched vertical cross-sections, as seen in tangential sections. Chambers in alternating superimposed positions and most approximately 0.2 mm high, with interwalls approximately 0.1 mm thick. Interwalls appear distinctly porous, with small interpores 0.01 mm in diameter locally preserved and locally abundant, making up over 50 percent of the volume of the walls. This may explain why walls are lighter gray and more crystalline-appearing than walls of the non-porous exhalant canals. Individual chambers in vertical sections appear essentially horizontal, but gently upward arched, narrowing prominently in upflexed end to the endowall. Nature of the exowall is uncertain, but it appears to be a continuation of the porous crystalline structure that characterized interwalls. Nature of ostia or perforations in exowalls uncertain because none is clearly cut in cross-sections.

Alaskan examples are branched sponges with subcylindrical stems 3.5–5.2 mm in diameter, most of which are approximately 5 mm in diameter, and at least 50 mm tall; branched dichotomously at intervals of approximately 10 mm with moderate regularity, but may be variable. Branches are monoglomerate around axial cluster of exhalant canals, clusters range from 1.2 to 2.2 mm in diameter, but most commonly approximately 1.5–2.0 mm in diameter, surrounded by chambers arranged in single layer forming walls 1.2–1.4 mm thick, composed of horizontal to upward-arched, radially arranged, long chambers, either somewhat spindle-shaped or slightly expanding radially; chambers are of same length as thickness of sponge wall, but 0.2–0.3 mm wide and 0.2–0.4 mm high, with generally spatulate to crudely hexagonal cross-sections at mid-wall, but becoming circular in cross-sections both near ectowall and endowall of sponge. Chambers are generally spaced 3 or 4 per mm, vertically, in longitudinal sections, and approximately 3 per mm measured horizontally around the outside circumference.

Cluster of axial canals is compact, of long straight to irregularly and weakly sinuous canals that range 0.2–0.3 mm in diameter, with most approximately 0.25 mm in diameter as circular tubular openings; canals are so spaced that axial cluster is 1.5 mm in diameter, cross-sections of 21 canals occur in cluster and 28 occur in axial cluster 2.0 mm in diameter. Clusters divide as sponge branches and form central cores of branches. Individual canals originate in lower parts as upturned tips of endopore tubes, but may have several endopore tubes empty into perforations vertically along stem. Walls of exhalant canals are approximately 0.05 mm thick, but may be somewhat thicker and with laminate filling structures in common junction areas between canals.
Single large endopore in endowall is at proximal end of each chamber; endopores are approximately 0.15 mm in diameter, generally arch slightly downward before bending sharply upward to enter one of exhalant tubes. Exhalant tubes, essentially diameter of endopore at base, expand upward to normal diameters approximately double that initial size.

Interwalls are approximately 0.08–0.10 mm thick through much of their length but may thicken to approximately 0.10–0.15 mm thick where they grade into endowalls and ectowalls of exterior. Exoxules are not preserved and presumably not developed. Ostia of exowalls are obscure in weathered preservations.

Discussion. — The Alaskan representatives of the species are virtually identical with those described from Silurian Ludlow rocks of the western slope of the Northern Ural Mountains in Russia. Alaskan specimens are moderately numerous. All Russian specimens are branching stems of monoglomerate sponges, whose cell-like chambers are arranged around an axial cluster of small tubular exhalant canals. Dimensions of the canals, dimensions of the chambers, and over all dimensions of the sponges confirm the identity of the species from the two widely separated occurrences.

*N. dichotomica* Myagkova 1955 contrasts to the new species, *N. hormathodes*, described here from southeastern Alaska, in having a more favose arrangement of the long chambers, rather than globose chambers, and in having considerably more numerous exhalant canals in the axial cluster. Mature parts of *N. dichotomica* may appear somewhat similar to initial juvenile parts of *A. textilis* Myagkova 1955, but the species and genera can be differentiated by the relative sizes of their chambers, which are several times larger in *Aphrosalpinx* than in *Nematosalpinx*, and in *Nematosalpinx* the axial cluster of exhalant canals penetrates completely through the branched sponges, rather than occurring only in the basal part, as in *A. textilis*. In that latter genus and species, the upper spongocoel is a tubular open structure, margined in intermediate levels with a somewhat verrucose layer or cluster of exhalant endopore tubes, and in the upper part by a grid-like cortex, or without a differentiated gastrostomal layer, where the endopores empty directly into the tubular open spongocoel. In *Aphrosalpinx*, thus, the central tubular spongocoel is retrosiphonate, whereas in *Nematosalpinx* the spongocoel is prosiphonate.

Material and occurrence. — Specimen 57–7/50, of Myagkova’s collection, now FM PE39869; a single thin section, but with sections of what may be 7 or 8 individuals in the stromatolitic algal limestone, from Ludlow age beds, Vishera River, the Urals. Excellent examples of the species also occur in algal- or microbial-encrusted growth forms, essentially in place, in samples from Locality 83RB40, from the Taylor Mountains D-2 quadrangle in southwestern Alaska. The species also occurs at Locality 83RB42 in the White Mountain area, McGrath A-4 quadrangle in western Alaska, but has not been observed in samples from other Alaskan localities.
Nematosalpinx hormathodes sp. n.
Figs 4A; 5F, H–L; 7; 8F–H.
Holotype: Thin section SB3-1WA-89, Fig. T.
Type horizon and locality: Ludlow part of Heceta Formation, Prince of Wales Island, northeast of Twin Mountain, locality SB3.
Etymology: Hormathos, Greek, chain of things, string or necklace, referring to the beaded, necklace-like stems of the small sponge.

**Diagnosis.** — Cylindrical to branched monoglomerate sponges with stems to 3 mm in diameter, single layer of globose chambers, alternatingly spaced, around axial exhalant canal cluster. Axial cluster approximately 0.5 mm in diameter with thin axial canals, 0.10–0.15 mm in diameter; chambers with branched intertubes and with distinct exaules generally 0.10–0.15 mm in diameter. Axial clusters with only few small canals, exaules essentially at mid-chamber height.

**Description.** — Relatively small aphrosalpingid sponge has cylindrical single to branched stems. Stems are to 2 or 3 mm in diameter, with axial cluster of convergent exhalant canals approximately 0.5 mm wide and with single layer of globose chambers in diagonal stacking around continuous axial exhalant canal cluster. Holotype is a regular longitudinal section of curved, branching form, on thin section SB3-1WA-89, irregular stem curves in and out of plane of thin section. Branch is somewhat smaller than on some paratypes, with diameters ranging to 1.7 mm in that part of the section where full diameter is represented. Axial cluster of exhalant canals is approximately 0.5 mm across, surrounded by small chambers up to approximately 0.7 mm wide, radially, and ranging from 0.5–0.7 mm high, longitudinally, and to 0.9 mm wide, measured parallel to circumference.

Individual thin axial canals are 0.10–0.15 mm in diameter in the lower part of stem; tubes lead upward from small exhalant pores or canals, which range to 0.17 mm wide, located in upper interior margin of each chamber. As in other sections, where thin sections cut tangential to axial canal, positions of exhalant pores are indicated by vesicula-appearing structure or by vesicular interruptions of the walls.

One moderately well-preserved branched intertube extends in from ostium approximately 0.15 mm in diameter; that opening expands to branched tip in center of chamber. Partial chamber below with distinct exaulos that extends approximately 0.5 mm, radially, from ostium approximately 0.15 mm in diameter at the wall, but exaulos tube appears to taper distally, to diameter of approximately 0.1 mm, where it is lost in section. Other circular impressions of exaules of same general dimensions appear to extend from chambers of branch, but bases are not cut in plane of thin section. Exaules sections are generally circular to slightly ovoid and 0.10–0.15 mm in diameter with characteristic thin walls. A few exaules may occur as clusters of small openings approximately 0.08 mm in diameter, where 2 or 3 are grouped together; solitary exaules tend to be larger tube-like openings.
Sections of the axial exhalant canal cluster merge upward, but in irregular sections they appear as discontinuous, which is unlikely unless lower chambers are abandoned, but no evidence suggests that.

Moderately well preserved paratype, on SB3-4EA2b-92, is steep sub-longitudinal section of a sponge at least 7 mm long and with a maximum diameter of approximately 2 mm. Individual globose chambers range from 0.4–0.6 mm high and 0.6–0.7 mm wide, radially from the axial cluster to the outside wall. Chambers of essentially same dimensions are seen in tangential sections, which would suggest more or less hemispherical chambers parallel to circumference of sponge.

Most chambers have minor vesiculae, which appear related to possible exaules that extend out from major ostium of each chamber. Moderate intertubes are developed in species. Many chambers, however, appeared to have only bubble-like vesiculae, at least in sections available.

Upper part of endowall in each chamber is perforated by single coarse ostium, 0.25–0.30 mm in diameter, which leads to exhalant tube that connects to vertical canals of axial cluster; these canals converge and merge to produce central porous region. Exhalant canals in small specimens range to 0.5 mm in diameter but are commonly smaller, except in the zone where canals converge to form vertical exhalant tubes.

Tangential slice through ectowall of one globose chamber, exposed below the principal sponge, shows wall exterior to be somewhat micronodose, with individual nodes separated by either grooves or limited canals that extend part way into walls, as in *Palaeoschinda*. Nodes on exteriors of chambers, with bases approximately 0.04 mm in diameter and rounded nodes, may extend up to 0.02 mm out from general surface of wall. Nodes are approximately 0.02–0.03 mm apart. This somewhat deep separation appears as pores in part of skeletal structure, but these openings do not continue through dense laminate inner layer of exowalls. Openings between nodes, however, do not penetrate through microgranular inner layer, either as seen in tangential section or in vertical sections through wall in upper part of sponge.

Porous outer layer does appear to continue as light second layer from exterior across upper part of interwalls of upward bulging chambers. Some areas suggesting nodose exterior may be function of overgrowth by encrusting algae. Where two layers of wall are well-exposed, and where section cut directly through the wall, wall is approximately 0.6–0.8 mm thick; of that, approximately 0.02–0.03 mm is relatively light layer, which appears to be continuation of outside tubular or nodose layer; remainder of wall is made of relatively dark, microgranular or microcrystalline laminate layers. Chambers have only limited chamber lining, so no inner laminar lining of chamber burying light colored layer, as developed in other associated species. Position of the exhalant tubular canal is indicated by forked, almost dentate lateral margins of the opening or by a circular extension of the laminated part of the wall along the upper inner edges of the chambers, even where pores do not appear.
Fig. 7. Generalized reconstruction of *Nematosalpinx hormathodes* sp. n., a branching species composed of a single layer of globular chambers arranged around an axial complex of a cluster of exhalant tubes that continue through the sponge. Irregularly curved exaulos and intertubes may be developed and may be preserved in sections of the chambers, as shown in the lower part. Diagonal sections may show exaulos and intertubes in chambers, like those in the upper left branch, or exaulos may appear only as circular interruptions like that in the tangential section at the top. Endopores are prominent, moderately coarse, openings through the endowall into the exhalant canal cluster, as shown in the section in the lower part and in the upper left branch. Stems are usually only a few millimeters in diameter.

One chamber shows moderately well-defined exaulos that extends perhaps 0.1 mm into chamber as circular tube, but extends approximately 0.5 mm out from the outer wall as thin, delicate tube, 0.10–0.12 mm in diameter. Tube walls are approximately 0.02 mm thick in proximal part, but thin to approximately 0.01 mm at distal tip.

What appear as transverse sections of exaulos occur below sponge in section and suggest exaulos to be moderately common as inhalant openings in wall; these, like ones attached to sponge are approximately 0.5–0.6 mm in diameter and with thin, dense laminate walls. Sections appear as cut lateral extensions from continuation of sponge, not cut in thin section, and suggest that sponge may have been as much as 3 mm longer or higher than preserved section. Similar sections of exhales occur above upper end of sponge and suggest that specimen may have been 2 mm longer above part preserved in section.
A branching specimen on thin section SB2-7.5EA5B-92 has chambers of essentially same dimensions as other specimens but is clearly branched in at least two places. Stem has somewhat narrower central axial cluster, approximately 0.3 mm wide. Entire branches at that point are only 1.5 mm in diameter, and most of sponge here is cut in moderate tangential section. Sponge has characteristic impressions of exhalant openings into the axial cluster, as well as moderate exaules, and with micronodose exowalls, as seen in tangential sections or where section cuts at low angles through walls.

**Discussion.** — Diagnostic features of the species include the axial cluster of only a few small canals; the high globose chambers with exaules essentially at midchamber, the exhalant openings at the upper inner margin of the chambers, and the micronodose character of interwalls and exowalls. Only limited vesiculae are developed and these appear to be possibly related to endotubes, but that is uncertain and simple vesiculae may be developed. The species differs from the large *Palaeoschada crassimuralis* Myagkova 1955 by differences in sizes of the chambers, dimensions of the central openings, and dimensions of the intertubes and exaules, as well. This species is smaller in dimensions throughout.

*Cyathothalamiella alaskensis* sp. n. has a single large axial canal and also has large chambers with somewhat irregular angulated walls. *C. irregularis* sp. n. has almost undulating, irregularly uneven chambers, in a pattern significantly different than the relatively smooth globose small chambers seen here.

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Fig. 8. Aphrosalpingid sponges from the Ludlow part of Heceta Formation of southeastern Alaska. A-D. *Cyathothalamiella alaskensis* sp. n., holotype SB3-4EA2d-92. A. Steep diagonal section with open spongocoel, surrounded by moderately thick-walled, globose chambers with exowalls perforated by large ostia, which lead distally to exaules and proximally to intertubes, both developed as thin-walled tubes, coarse endopores occur in the inner, upper edges of the chambers and lead to the simple, open tubular spongocoel; endowall laminate; x 5. B. Enlargement of tangential cut through wall of the spongocoel showing the distinct laminate lining and the darker original endowalls around the spongocoel and in interwalls between chambers; x 25. C. Enlargement of the laminate endowall perforated by a single large endopore, in the upper inner margin of the chamber, which connects the open chamber, on the right, to the tubular spongocoel, on the left; x 25. D. Enlargement of a branched intertube, within the chamber, and the exaules as a continuation from an ostium in the exowall; x 25. E. *Aphrosalpinx textilis* Myagkova 1955. Specimen SB2-FL2A-89, transverse section showing part of the circular, tubular spongocoel, in the lower left, and cell-like chambers, on the right; endopores of inner ends of the chambers connect to the tubular spongocoel; short tube-like exaules were cut somewhat diagonally along the outer edge, in the upper and lower right; x 10. F-H. *Nematosalpinx hormathodes* sp. n. F. Holotype enlargement of the upper part of Fig. 5I showing globular chambers, with denticulate upper margins indicating positions adjacent to the endopores, one of which is moderately well-developed in the lower left chamber (arrow), connected to one of the subvertical, somewhat serpentine exhalant canals of the axial cluster, in the lower left; x 25. G. Diagonal section of lower part of the same specimen showing globular chambers arranged in a layer around the multiple exhalant canals of the axial cluster, in the center; one endopore, of the large chamber in the lower right, opens into one
of the axial exhalant canals (arrow); x 25. H. Specimen SB3-4EA2b-92, enlargement of the lower part showing the globular chambers with thick walls and with prominent endopores (arrows) emptying into multiple exhalant tubes of the central axial complex; x 25.
This species contrasts sharply to *Aphrosalpinx textilis* Myagkova 1955 by having generally smaller dimensions, simplicity of only a few canals in the persistent axial cluster, long cylindrical branching stems, and lack of a complex differentiated wall. *Aphrosalpinx* has a broad open axial spongocoel in the upper part of the obconical individuals.

Among sphinctozoans described from elsewhere in the stratigraphic section, small species of *Cystothalamiella* are superficially similar, but that genus has chambers arranged in two or more layers around the canal axial complex, and also has distinctly porous walls without exaxules or intertubes. At first glance, the species may appear similar to longitudinal sections of small species of *Vesicocaulis* (Ott 1967; Senowbari-Daryan 1990), but that Triassic sponge has ring-like chambers around the axial canal complex, rather than the glomerulate structure seen here.

*Diecithalamia* Senowbari-Daryan 1990 is a monoglomerate sponge with an axial canal cluster, but that sponge appears to lack exaxules and intertubes and to have porous walls, although it does have the peculiar ostia associated with excurrent openings in the upper inner margin of the chamber walls. *Discosiphonella* Inai 1936 is a monoglomerate sponge from the late Paleozoic, but it has a porate form and also lacks the numerous exhalant canals of the axial region. It is significantly larger and has distinctly porous walls, although it does have a micronodose-appearing exterior to the ectowalls and interwalls. *Discosiphonella* has a fundamental structure significantly different from the well-defined exaxules-bearing sponge described here.

The new Alaskan species differs from the type species, *Nematosalpinx dichotomica* Myagkova 1955 in having relatively larger, more globose chambers, and far fewer exhalant canals in the axial clusters. Both species...
lower left, irregular thick-walled chambers, in the center, and part of thin-walled exaules in the upper right; × 10. G. Specimen MC-Oal-89. transverse section showing single layer of chambers with prominent curved exaules on their distal margins and a laminate, tubular, vesiculate central spongocoel; prominent exaules extend from chambers as open tubes from large ostia; × 10.
are small sponges, however, with branched stems generally less that 5 mm in diameter but several cm high.

**Materials and occurrence.** — Holotype SB3-1WA-89, paratypes on thin sections CP-3-89, MC-FL2C-89, SB1-10-89, SB1-27-89, SB2-4E-89, SB2-7.5EA5b-92, SB3-2E-89, and SB3-4EA2b-92, all from the Silurian Heceta Formation from southeastern Alaska.

Genus **Cystothalamiella** Rigby & Potter 1986

Type species: **Cystothalamiella dacta** Rigby & Potter 1986.

**Diagnosis.** — 'Obconical to conical-cylindrical, small stems made of agglomerate polygonal or arcuate chambers with imperforate walls around the central, very coarsely tubular spongocoel. Tubular exaules well-defined, one or two per chamber, may extend a short distance into the chamber and may be somewhat open or trumpet-like with a craticula screening the distal opening.' (Rigby & Potter 1986: 32)

**Discussion.** — The geologic range of **Cystothalamiella** is extended from the Ordovician into the Silurian. The type species, **Cystothalamiella dacta** Rigby & Potter 1986, was described from Ordovician rocks in the Klamath Mountains of northern California.

**Cystothalamiella alaskensis** sp. n.

Holotype: Thin section SB3-4EA2d-92.

Type horizon and locality: Ludlow part of Heceta Formation, Prince of Wales Island, northeast of Twin Mountain, locality SB3.

Etymology: Alaskensis, named for Alaska, the state where the species was found.

Figs 8A–D.

**Diagnosis.** — Monoglomerate subcylindrical sphinctozoans with globular chambers to 2.5 mm high around central tube approximately 1.0 mm in diameter, with stem diameters 4.0–4.5 mm; thin-walled tubular exaules and long intertubes well developed, generally one per chamber. Intertube tips branched, lacking craticula.

**Description.** — Single specimen in collection is a small fragment, roughly 9 mm long, consisting of large central tube, approximately 1.0 mm in diameter, surrounded by single layer of globular chambers. Diameters of stems range 4–4.5 mm in general cylindrical form with exaules extending up to 1.5 mm out beyond that. Chambers have both coarse incurrent and excurrent ostia, and with both intertubes and exaules. Walled central tube extends in prosiphonate fashion approximately 1.5 mm beyond upper chambers. Chambers are 2–2.5 mm high, somewhat irregular, not smooth globose, with dense walls approximately 0.11 mm thick.

Exaules extend at least 1.5 mm out from ectowall, and intertubes extend approximately same distance into interior. Intertubes are bifurcated with several openings in thin, dense, laminated wall. Relationship within these chambers suggests that openings were excurrent through somewhat narrowed ostia. Approximately 0.2 mm inside of ostia intertubes expand to approximately 0.4 mm in diameter before narrowing to
branched tips, with openings in those tips 0.1–0.2 mm across. Tranverse sections of intertubes in individual chambers appear as thin floating vesiculae in cement-filled chambers. Exaules on exterior expand abruptly to allantoid shapes and to approximately 0.5 mm in diameter, to continue to single distal openings approximately 0.4 mm in diameter.

In upper part of specimen, endowall, or wall of central tube, cut diagonally, and shows as a distinctly laminate structure; thickness of endowall diminishes upward from maximum of approximately 0.6 mm to feather edge approximately 0.05 mm thick before lost in crystalline cement. Coarse endopores or ostia lead from chambers into central tube approximately 0.3 mm in diameter as openings to short exhalant intertubes. Latter may be as much as 0.5 mm long as circular extensions into chambers where openings may be approximately 0.2 mm across. These openings appear most common in upper part of chamber as tubular flexures where interwalls join endowalls around central tube. Some interwalls are distinctively laminate, with only obscure interruptions that may have been ectopores, approximately 0.05 mm in diameter.

**Discussion.** — *Cystothalamiaella alaskensis* sp. n. differs from associated sphinctozoan sponges from the Heceta Formation in having a prominent, single, tubular prosiphonate central tube and in having clearly excurrent and incurrent ostia in endowalls and ectowalls. It is similar to *Pala eoschada* in having intertubes that branch in chamber interiors. *C. alaskensis* also has exaules, which *Pala eoschada* apparently lacks. *Pala eoschada* also has a distinctively porous double-layered wall, in contrast to the more laminate, obscurely porous walls in the species of *Cystothalamiaella*. *Cystothalamiaella* contrasts with *Aphrosalpinx*, that characteristically has multiple exhalant canals in the axial region, although both may have intertubes and exaules.

The diagonal section of *C. alaskensis* appears somewhat similar to *Vesicocaulis giacolonensis* Senowbari-Daryan 1990 (Senowbari-Daryan 1990: Pl. 42: 3, 5), but *Vesicocaulis* has annular, rather than glomerate chambers, and appears to lack both intertubes and exaules that characterize *C. alaskensis*. In addition, *Vesicocaulis* has porous walls and does not have distinctive ostia like those well developed in *C. alaskensis*.

*C. alaskensis* is characterized by large globose chambers significantly larger than chambers in *Aphrosalpinx* or the associated *C. irregularis* sp. n. The latter occurs on the same sample with *C. alaskensis*, but in a different thin section. *C. irregularis* has significantly smaller chambers, smaller diameter exaules and intertubes, although it does have an irregular chamber form like *C. alaskensis*.

*Cystothalamiaella ducta* Rigby & Potter 1986 is a similar stem-like sponge composed of irregular chambers and with prominent exaules, but these radial extensions are funnel-like and may have craticula. In that Ordovician species the central tube has complex, discontinuous, vertical blade-like elements along the gstral margin. These structures are not developed in the Alaskan species, and the California *C. ducta* has a
retrosiphonate central tube, rather than a prosiphonate central tube, like in *C. alaskensis*. Endopores are more common in *C. ducta*, apparently with several pores per chamber, spaced so that 3 or 4 occur per millimeter horizontally and vertically in the endowall, rather than the single prominent tube-like endopore developed in each chamber of *C. alaskensis*.

*Cystothalamiaella craticulata* Rigby & Potter 1986 is composed of adnate to distant glomerate, spherical to subspherical chambers, around an indistinct spongocoel tube. That species has robust, stubby exaules that are thick-walled and infundibuliform with distal craticula. The species has a growth form and exaules that are distinctly different than the relatively regular form in *C. alaskensis*, a species which has relatively delicate, thin-walled, tubular exaules, unlike the Ordovician species from the Klamath Mountains.

*Cystothalamiaella tuboides* Rigby & Potter 1986 has even coarser, funnel-shaped, robust exaules, 1.5–1.8 mm in diameter at the base, in contrast to the delicate tube-like exaules in *C. alaskensis* that are approximately 0.5 mm in diameter. *C. tuboides* also has considerably larger chambers than in the relatively delicate *C. alaskensis*.

**Material and occurrence.** — Holotype on thin section SB3-4EA2d-92; Ludlow part of the Heceta Formation from southeastern Alaska.

*Cystothalamiaella irregularis* sp. n.

Figs 9C, F–G; 10; 11C–D, F.

Holotype: Thin section MC-8a3-89; Fig. 9.

Type horizon and locality: Ludlow part of Heceta Formation, Heceta Island, locality MC.

Etymology: *Irregularis*, Latin, irregular, referring to the uneven form of the species and its chambers.

**Diagnosis.** — Monoglomerate cylindrical stems with ragged spongocoel and angular-appearing chambers, producing stems approximately 6 mm in diameter, with only local exaules, to approximately 0.4 mm in diameter. Chambers locally separated, with upper walls thicker than lower, exaules developing intertubes within chambers. Chambers approximately 1 mm high, with somewhat irregular walls.

**Description.** — Holotype is steeply diagonal section on thin section MC-8A3-89; irregular cylindrical stem with relatively simple, open but ragged-appearing spongocoel, approximately 1 mm in diameter, surrounded by irregular single layer of uneven, often angular-appearing, chambers in a sponge approximately 6 mm in diameter and at least 14 mm high. Spongocoel is lined with laminar layer approximately 0.2 mm thick, distinct from irregular, almost crenulate inner ends of chambers. Chambers are approximately 1 mm high and extend in somewhat irregular fashion, approximately 2.5 mm out from spongocoel or endowall; thickness of chamber walls is irregular and thickest, to 0.2 mm thick, near gastral termination and openings into spongocoel around endopores. Latter are approximately 0.2 mm in diameter, as irregular curved openings
Fig. 10. Generalized reconstruction of Cystothalamietta irregularis sp. n., showing relationships of the irregular chambers to the tubular open spongocoel. Chambers are generally radially arranged, with one or two prominent ostia or exaules locally developed on the exterior. Prominent endopores in the thickened endowall open into the tubular spongocoel, which may be blocked with diaphragms marking interruptions in the growth of the sponge. Upper chamber walls tend to be thicker and less crenulate than the lower chamber walls. Sponge stems usually 1–2 cm in diameter.

that rise steeply upward from inner end of chambers and then empty into spongocoel, more or less horizontally, as simple untubed openings.

Exaules are only locally developed or preserved on fragments as tubular openings approximately 0.3 mm in diameter, with walls approximately 0.05–0.06 mm thick so entire tubular structure is approximately 0.45 mm in diameter. Exaules extend into interior as intertubes of essentially same dimensions, although with walls somewhat thinner and only locally developed. Chambers are commonly in mutual contact, but locally, gaps in structure occur between chambers so texture of sponge is moderately open, in part, but compact and chamber-on-chamber in other parts. Such irregularity is also evident in tangential paratype sections and other sections of sponge. Small Aphrosalpinx nana is attached to side of holotype and chambers are distorted around it.

Some upper interwalls are thicker and more continuous than apparently secondarily added lower encrustations of chambers, which have uniformly crenulate to irregular basal margin. Some crenulate surfaces are traceable across sponge as though marking cessation planes or surfaces
of stylolitic-type solution, before subsequent chambers are formed. Diaphragms or horizontal vesiculae block open spongocoel and extend, more or less, from laminate wall to laminate wall.

Stems are subcylindrical with prominent axial tube, surrounded by single layer of characteristically irregular, almost subangular, rounded chambers, chamber walls of varying thickness. Chambers are generally 0.4–0.6 mm high but may be up to 2 mm across with sagging, irregularly undulate walls. Vesiculae or intertubes are relatively rare.

Tubular exaules extend from ostia in chamber walls to 1 mm long with irregular trends. Intertubes and exaules have delicate thin walls, 0.01–0.02 mm thick, but with irregularity on individual tubes thicker where walls deflect angularly. Vesiculae in chambers are essentially the same thickness as exaules walls but with cyst-like development less clearly related to intertubes or exaules.

Chamber walls are dense although with irregular outer layer that commonly appears lighter than dense inner part. Chamber walls are 0.6–0.8 mm thick, with considerable variation along individual walls; interwalls are thickest where moderately sharply flexed or with angular outer expression. Moderately clear layer, perhaps of diagenetic origin, is approximately 0.02 mm thick, but its consistent occurrence suggests some original mineralogic difference or textural difference between inner and outer or upper parts of the interwalls. Tangential view of one chamber wall, near the base, shows possible pores 0.01–0.02 mm in diameter in microcrystalline dense walls, but pores are not evident in other areas, and apparent pores may be only differences in microcrystallinity.

Discussion. — Cystothalamiella irregularis sp. n. differs from associated species in dimensions of individual chambers and its crenulate to uneven, often sagging or angularly flexed, walls. Because some available sections

Fig. 11. Aphrosalpingid sponges from the Ludlow part of Heceta Formation, Alaska and Vishera River, the Urals. QA-B. Nematosalpinx dichotomica Myagkova 1955, FM PE39869 from Myagkova collections; x 10. A. Monogglomerate radial chambers around thick-walled exhalant canals, in branched reference specimen. B. Near-longitudinal view showing outer cellular chamber layer and inner thick-walled exhalant canals. QC-D. F. Cystothalamiella irregularis sp. n. C. Holotype, MC-6a3-89, with irregular chambers around laminated spongocoel and with associated Aphrosalpinx nana sp. n. along the left margin; x 3. F. Same enlarged, showing laminate walls of the irregular central tube and surrounding irregularly-shaped chambers, from which extend irregular exaules (e) from outer margins of irregular exowalls; endopores (larger arrows) connect chambers to the spongocoel through thickened endowalls, openings are cut in vertical sections in the upper part and appear as dark, broad rings; lower irregular parts of chamber walls appear thin and almost stylolitic; diaphragms (d) extend across the spongocoel in the lower part; light layers in the walls (small arrows) may be a result of diagenesis or of differing skeletal materials. D. Specimen SB3-4EA2b-92, tangential view through part of the outer chambers showing the characteristic irregular form, with curved exaules extending distally from the chambers; possible endopore tube (arrow) shows at the upper, inner, edge of one of the lower chambers; x 5. DE, G. Aphrosalpinx textilis Myagkova 1955, specimen FM PE39867 from Myagkova collection; both x 10. E. High-angle tangential section showing cell-like chambers and elongate exaules in the lower center. G.
Diagonal section through monoglomerate chamber layer, in the lower part, to the spongocoel in the upper part, where lined with a finely porous or tubular vermiculate-appearing layer.
are tangential, relationships to other structures, such as the axial canal complex, are uncertain in those specimens, although presence of exaules and limited intertubes is evident.

Irregularity of the chambers, the lined simple broad tubular spongocoel, which may be partially filled with vesiculae, and the irregular thin-walled exaules are characteristic of the species and genus and differentiate it from the considerably more regular *Aphrosalpinx textilis* Myagkova 1955. The irregular species is considerably coarser than *A. nana* sp. n. Chambers are not as globular as in *Cystothalamiaella alaskensis* sp. n., which appears to have an open spongocoel and moderately coarse endopores, to 0.4 mm in diameter. Both forms may have vesiculae or intertubes and exaules. It is principally the dimensions of the somewhat irregular chambers and the nature of the spongocoel that are utilized to differentiate these latter forms.

*Cystothalamiaella irregularis* sp. n. has chambers somewhat smaller than those in *Cystothalamiaella ducta* Rigby & Potter 1986 and has a more irregular outline than the distinctively smooth rounded exterior seen in type specimens of *C. ducta*. Both species have prominent exaules, but those in *C. ducta* rise from a conical mound rather than from a constricted ostium like that in *C. irregularis*. The Alaskan species also lacks the complex, discontinuous, vertical bladelike elements characteristic of the gastral margin of the spongocoel in *C. ducta*.

*Cystothalamiaella irregularis* contrasts with *Cystothalamiaella craticulata* Rigby & Potter 1986 in having distinctively smaller chambers that produce
position. The regular cell-like chambers are shown in tangential view in the lower central part, but in radial longitudinal view in the upper middle part, where the axial canal cluster also shows well; × 2.
a smaller diameter stem and in lacking the radially expanded buccinal exaules, which have characteristic craticula in C. craticulata. The species are somewhat similar, however, in having a somewhat adnate glomerate structure to the stems.

C. tuboides Rigby & Potter 1986 has chambers that are several times larger than the small chambers in C. irregularis, for chambers in C. tuboides are generally 5.0–7.5 mm wide and 5 mm high. That California species also has very coarse exaules which expand abruptly into funnel-shaped structures, in contrast to the fine tubular exaules in C. irregularis.

**Material and occurrence.** — Holotype on thin section MC-8a3-89, paratypes on thin section SB3-4EA2b-92 and MC-Oal-89; possibly related irregular clusters of chambers occur on CP-4-89 and YP58-2FL-92, but chambers of the latter do not have quite the same irregularity as chambers in other sections. Other specimens included in the species with some question occur on thin sections MC-2a-89; RP-FL8-(-88); and SBf -f O-89. Ludlow part of the Heceta Formation, southeastern Alaska.

Subfamily Palaeoschadinae Myagkova 1955

**Discussion.** — Myagkova (1955a) described the genus Palaeoschada from Silurian rocks exposed on the western slope of the Ural Mountains and placed the genus within the aphrosalpingid archaeocyathans. She erected the family Palaeoschadidae to include the genus, and to separate it from Aphrosalpinx and Nematosalpinx that also occur in the Russian Silurian rocks and that she also described. She (Myagkova 1955a) differentiated these forms within the order Palaeoschadiformes, a new order characterized by skeletons of thick-walled chambers, which contain well-developed vesicular tissues, chambers whose walls are pierced by numerous pores. The family was further described, as translated, as being characterized by 'Cells are irregularly arranged to form tubes. The only genus is distinctive.' In the original copy of the paper that we have, the order Palaeoschadiformes is altered into Palaeoschada. This altered spelling is followed in all subsequent publications of Myagkova.

There is little question that the outer layer of the chamber walls have large pores, but thin sections show that those pores do not penetrate through the laminated inner layer. For this reason, the palaeoschadid sponges are here tentatively placed within the Aporata and within the family Aphrosalpingidae, but in a distinct subfamily.

**Genus Palaeoschada Myagkova 1955**

*Type species:* Palaeoschada crassimuralis Myagkova 1955.

**Palaeoschada crassimuralis Myagkova 1955**

Figs 9A–B, D–E; 11.

*Palaeoschada crassimuralis* sp. n.; Myagkova 1955a: pp. 480–481, Fig. 2a–b.

*Palaeoschada crassimuralis* Myagkova; Vologdin & Myagkova 1962: p. 137, Pl. 9, Fig. 8; Fig. 128a–b.
Fig. 13. Generalized reconstruction of *Palaeoschada crassimuralis* Myagkova 1955, showing globose chambers, each with a prominent ostium in the ectowall and with endotubes that may branch in the interior of the chambers. Prominent endopores connect into one of several coarse vertical canals of the axial exhalant cluster. Chamber walls are characteristically double-layered, with an inner dense microcrystalline layer, and an outer, coarsely perforate, more ragged-appearing layer. A third layer may develop on interwalls where the interior layer of a succeeding chambers may coat the porous upper layer of the endowall. Stems may be approximately 1 cm in diameter.


**Emended diagnosis.** — Irregularly subcylindrical sphinctozoans with irregular central tube, around which one layer of globose, upward arcuate, cystlike chambers forming walls; chamber walls double-layered, inner dense layer with only fine scattered pores and outer layer with coarse abundant pores. Ectowalls with large circular ostia, intertubes extending irregularly into chamber interiors and possibly branching; exaules wanting; endopores obscure.

**Description.** — Best-preserved figured specimen upward expanding, irregularly cylindrical to curved stem, approximately 4 mm in diameter at base, expands to 7 mm in diameter at preserved top. Stem is of single layer of globose, upward arcuate, cyst-like chambers one layer thick around central tube or canal. Central tube is irregular, 0.5–0.6 mm in diameter in lower irregularly tangential section, but 1.5–2.5 mm wide in nearly complete upper part of sponge. Exterior is cystose, marked by each individual bulging chamber. Chambers increase in size upward from 1.5 to 2.5 mm
high and from 2.5 to 3.5 mm wide. Chambers are more or less diagonally spaced, but not in regular predictable pattern.

Exowalls are pierced by coarse ostia, 0.5–0.6 mm in diameter with most approximately 0.5 mm across, defined by inward deflection of laminae of ectowall. Laminae continue into chamber interiors forming tubelike intertube extensions of ostia. These gradually taper and may branch, with opening at tip of each branch. Chambers with common irregular vesiculae appear cystose to tubular.

Ectowalls and interwalls are double-layered, with prominent, coarsely porous, outer layer and a dense, more finely perforated inner layer. Ectowalls are generally 0.2–0.3 mm thick but interwalls may be up to 0.4 mm thick where composed of three layers. Inner dense layer is 0.10–0.15 mm thick in up-arched interwalls and somewhat less thick, 0.10 mm or less, in lower parts of ectowalls; layer is perforated by scattered pores mostly 0.02 mm in diameter, but ranging from 0.015 to 0.025 mm across. Most pore openings are straight but some are irregularly curved and expand into larger pores in outer porous layer. Inner layer is commonly irregularly laminated, in units 0.01–0.02 mm thick. Some areas of inner layer appear microtubular, but perhaps are only aligned crystals or sphaerolites; these stacked elements locally occur 3–4 per 0.2 mm measured parallel to the under surface of the inner wall.

Pores of outer layer are 0.03–0.06 mm in diameter, with most approximately 0.04 mm across; mostly 0.02–0.03 mm apart, separated by dense skeleton. Pores generally are perpendicular to walls, but variable and curved to as much as 60 degrees from normal to wall trend. Pores may branch distally or be cross-connected in middle part of outer layer by canals of same general diameter, producing reticulate openings in layer, which is generally 0.10–0.15 mm thick, but locally expands to 0.25 mm thick. Outer surface may be irregularly nodular or with sharp conical peaks, but generally these structures lose distinction in middle part of wall.

Third layer may occur as lining over interior of chambers; layer was added as sponge grew vertically; third layer is of variable thickness, generally thickest near wall junctions and thinnest towards endowall; layer ranges to 0.2 mm thick and laminate; laminae continue laterally into vesicles or as intertube structures. Lining layer generally sealed off interpores and isolated chambers in structure.

Exaules are not developed around ostia. Central tubes may be compound with two or three exhalant canals in the axial area, producing an irregular section which is cut diagonally at base and with three or more distinct openings at summit where it is also cut somewhat diagonally.

Discussion. — The species is most similar in general growth form and appearance to such sponges as Cystothalamia, but it has only one layer of chambers, such as in characteristic of Discosiphonella or Cystauletes. Both Cystauletes and Discosiphonella, however, have very porous walls in which pores extend completely through interwalls, endowalls, and ectowalls. Both of these genera have tubular, broad central spongocoels, and
Fig. 14. Photomicrographs of unidentified lithistid sponges on thin section SB3-4EA2b-92, Heceta Formation, Prince of Wales Island, Alaska. Both A and B show a moderately regular network of what appear to be dendroclones (arrows), preserved as moderately coarsely crystalline, light-gray carbonate in medium-gray calcareous matrix. Arrow in A points to what appears to be a trab. connected by a rod-like dendroclone to a second trab that appears like others in the moderately regularly spaced series throughout the sectioned fragment. The upper arrow in B points to a trab. apparently connected to adjacent trabs by a Y-shaped dendroclone. Large lower arrow in B points to what probably is a trab connected to adjacent trabs by rod-like or J-shaped dendroclones. Both figures x 25.

both may have vesiculae as infilling structures, but they lack the distinctive intertubes within the chambers such as are characteristic in *Palaeoschada*.

Intertubes appear to have been excurrent in *Palaeoschada*, based on the general enlargement of those tubes towards ostia and on the convergence and enlargement of the branched tips of those tubes within the interior of the chambers. Water must have circulated in through the pores, limited as they were, and out through ostia. This may explain why endopores are so poorly developed and their relationships to multiple, vertical exhalant canals of the axis, are obscure. Senowbari-Daryan (1990: Fig. 52) showed this type of branched excurrent system exemplified by *Celyphidia submarginata* (Münster 1841). That genus, however, is moniliform and without a central axial tube. It also lacks the double-layered wall characteristic of the Silurian sponges described here.

*Palaeoschada* is similar to some species of *Cystothalamia* in having multiple exhalant canals in the axial region, but differs from those forms
in being monoglomerate, that is, with only a single layer of chambers around the central tubes. The associated Aphrosalpinx also has multiple exhalant canals in the axial cluster and only a single layer of chambers around that cluster, but Aphrosalpinx has a distinctly different wall, generally lacking the prominent intertubes and with numerous well-developed exaules.

**Material and occurrence.** — Figured specimen on thin section SB3-7E FL1-90, Ludlow part of the Heceta Formation of southeastern Alaska, supplements the original collection from the Ludlow of the Northern Ural Mountains, Russia.

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**References**


Alaskan Aphrosalpingid Localities

West-Central Alaska: McGrath 1:250,000 quadrangle


Alaska and Aphrosalpingid Localities

West-Central Alaska: McGrath 1:250,000 quadrangle

79WG211. — Crest of WNW-trending ridge line at approximate elevation of 2,700 feet, 0.12 mile south of north edge of line separating NW1/4 and NE1/4 of NW1/4 sec. 12, T. 24 N., R. 31 W., McGrath A-4 quadrangle. Lat. 62°11'25" N., Long. 154°53'00" W. Locality same or very close to 83RB42. Collector, W.G. Gilbert, 1979 (Fig. 2B).

83RB41. — Talus along crest of WNW-trending ridge at an approximate elevation of 2,600 feet. SW1/4, NE1/4, NW1/4, sec. 12, T. 24 N., R. 31 W., McGrath A-4 quadrangle. Lat. 62°11'23" N., Long. 154°52'53" W. Collector, R.B. Blodgett, 1983 (Fig. 2B).

83RB42. — Talus and outcrops of prominent cliffy exposures along crest of WNW-trending ridge line at approximate elevation of 2,700 feet, 0.12 mile south of north edge of line separating NW1/4 and NE1/4 of NW1/4, sec. 12, T. 24 N., R. 31 W., McGrath A-4 quadrangle. Lat. 62°11'25" N., Long. 154°53'00" W. Locality same or very close to 79WG211. Fossils include aphrosalpingids and tabulate corals. Collector, R.B. Blodgett, 1983 (Fig. 2B).

Southwestern Alaska: Taylor Mountains 1:250,000 quadrangle

83RB40. — East side of hill 1562, just below summit (elevation approximately 1500 feet), SW1/4, SE1/4, SW1/4, sec. 28, T. 10 N., R. 41 W., Taylor Mountains D-2 quadrangle. Lat. 60°55'22" N., Long. 156°33'50" W. Collector, R.B. Blodgett, 1983 (Fig. 2C).

South-Central Alaska: Talkeetna Mountains 1:250,000 quadrangle

74AR83 (=USGS 9721-SD). — Marbleized limestone exposed along northeast-trending ridge northeast and downslope of high point (elevation 5270 feet) at south edge of SW1/4, SE1/4, SW1/4, SE1/4, sec. 14, T. 28 N., R. 19 W., Talkeetna C-6 quadrangle. Lat. 62°30'35" N., Long. 133°44'22" W. Collector, B.L. Reed, 1974 (Fig. 2D).

Southeastern Alaska: Craig 1:250,000 quadrangle

67A0v1422 (=USGS 8053-SD). — Hoot Island, 2,000 feet along shore southwest of triangulation station Hoot, NW 1/4, SE1/4, SW1/4, SE1/4, sec. 13, T. 69 S., R. 78 E., Craig D-5 quadrangle. Lat. 54°53' N., Long. 133°23'14" W. Collector, A.T. Owenshine (Fig. 2E).

MC. — Heceta Island, along the north shore, outcrop adjacent to road above boat dock and ramp in a small inlet southwest of Camp Island and across Heceta Island northeast of the head of Warm Chuck Inlet, NW1/4, NW1/4, NW1/4, sec. 13, T. 70 S., R. 78 E., Lat. 55°47'30" N., Long. 133°29'40" W., Craig (D-5) quadrangle. Collector C.M. Soja (Fig. 2F).

RP. — Tuxekan Island, along the east shore, approximately 500 meters northwest of small triangulation station, Bruce, SW1/4, NE1/4, NW1/4, sec. 13, T. 70 S., R. 79 E., Lat. 55°48'20" N., Long. 133°14'00" W., Craig (D-4) quadrangle. Collector, C.M. Soja (Fig. 2G).

YP. — Tuxekan Island, east shore, west of triangulation station, Bruce, on Yahku Point northeast of Yahku Cove, SW1/4, SE1/4, NW1/4, sec. 13, T. 70 S., R. 79 E., Lat. 55°48'10" N., Long. 133°14'00" W., Craig (D-4) quadrangle. Collector, C.M. Soja (Fig. 2G).

CP. — Prince of Wales Island, shore on east side of Tuxekan Passage, north from Cedar triangulation station approximately 800 meters, in center of SE1/4, sec. 18, T. 70 S., R. 80 E., Lat. 55°47'50" N., Long. 133°12'00" W., on the Craig (D-4) quadrangle. Collector, C.M. Soja (Fig. 2G).

SB1. — Prince of Wales Island, along the Forest Road, northwest of Twin Mountain, NE 1/4, SW1/4, SW1/4, sec. 17, T. 70 S., R. 80 E., at Lat. 55°47'45" N., Long. 133°11'15" W., on the Craig (D-4) quadrangle. Collector, C.M. Soja (Fig. 2G).

SB2. — Prince of Wales Island, quarry exposures along the western Forest Road, east of Nundei Cove and northwest of Twin Mountain, NW1/4, SE1/4, NE1/4, sec. 19, T. 70 S., R. 80 E., Lat. 55°47'15" N., Long. 133°11'45" W., Craig (D-4) quadrangle. Collector, C.M. Soja (Fig. 2G).

SB3. — Prince of Wales Island, quarry exposure along the Forest Road, approximately 300 meters southwest of SB2, northwest of Twin Mountain, SE1/4, SW1/4, NE1/4, sec. 19, T. 70 S., R. 80 E., Lat. 55°47'10" N., Long. 133°12'00" W., Craig (D-4) quadrangle. Collector, C.M. Soja (Fig. 2G).
Streszczenie