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A Review of Recently Discovered Remains of the Pleistocene Branchiopods (Anostraca, Notostraca) from NE Siberia and Arctic Canada

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Abstract: In this study, we examine, identify, and discuss fossil remains of large branchiopod crustaceans collected from six sites across the Beringian region (north-eastern Asia and north-western North America). Eggs and mandibles from Anostraca and Notostraca, as well as a notostracan telson fragment and a possible notostracan second maxilla, were collected from both paleosediment samples and also from large mammal hair. The remains of large branchiopods and other species that are limited to seasonally astatic aquatic habitats (temporary wetlands) could be useful indicator organisms of paleoecological conditions. Different recent large branchiopod species have very different ecological preferences, with each species limited to specific geochemical component tolerance ranges regarding various salinity, cation, and gypsum concentrations. Our purpose is to bring the potential usefulness of these common fossil organisms to the attention of paleoecologists.

Keywords: Beringia; Pleistocene; fossil; Anostraca; Notostraca; paleoecology; temporary wetlands

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1. Introduction

The Branchiopoda are a class of crustaceans that primarily inhabit seasonally astatic aquatic habitats (temporary pools). The class is comprised of Anostraca (fairy shrimps), Notostraca (tadpole shrimps), and the superorder Diplostraca, which is further subdivided into Laevicaudata (smooth clam shrimp), Spinicaudata (spiny clam shrimp), Cyclestherida (tropical clam shrimp), and Cladocera (water fleas). All of these groups, except Cladocera, are collectively referred to as "large branchiopods" [1], although this common name has no phylogenetic or taxonomic basis. These large branchiopod crustaceans have been found from various fossil strata, with the oldest representatives being putative anostracans reported from Cambrian [2]. The earliest large branchiopod communities, consisting of all three main branches, Anostraca, Notostraca, and Diplostraca, represented by spinicaudatan clam shrimps, were reported from the Upper Devonian [3–6]. The earliest putative cladocerans fossils come from the Paleozoic; however, these records are dubious [7]. Earlier cladoceran fossils may have been missed due to their small size and poor fossilization. The earliest confirmed fossil cladocerans come from the Mesozoic and were found co-occurring with large branchiopods [7–10].

Modern branchiopod crustacean adults are often difficult to collect due to the astatic nature of the habitats where they occur; when a given habitat is holding water and adult shrimp are swimming, the site may not necessarily be accessible due to mud, snow, ice, or inclement weather [11,12]. However, at practically any time, branchiopod eggs can be collected from the substrate [11–14] when access to a given site is less problematic. In

addition, egg dispersal vectors such as certain insects, birds, or large mammals can also be used as sources of branchiopod eggs [11,13,14].

Recently, there has been a series of publications on Pleistocene branchiopod fossils, focusing on the eggs and ephippia (modified molting exuvia of the anomopod cladocerans bearing resting eggs). Like modern branchiopods, fossilized eggs and body parts were found in Pleistocene ponds and lakes [15–19], temporary wetland sediment layers [20,21], and in the body hair of large mammal remains (mammoth and woolly rhinoceros) found in the Siberian permafrost [22–25].

These records have been used in efforts to determine and define paleolimnological environments. Typically, cladocerans have been used in these endeavors [15,19,20,26–28], and large branchiopods have only recently been used in these studies [21,22,25]. This is in part due to large branchiopods being primarily found in seasonally astatic aquatic habitats, while most recent paleolimnological studies have utilized large lake sediment cores.

In support of this approach, we present a brief review of a variety of recently identified large branchiopod fossilized remains from NE Siberia and NW North America. We hope that the material and identifications presented here will aid in future studies of these fossil organisms in both paleodiversity and paleoecology studies.

2. Materials and Methods

Seven previously collected samples from various Pleistocene localities across NW Canada and NE Russia (Figure 1) were studied by our team. These samples' specific details are as follows.

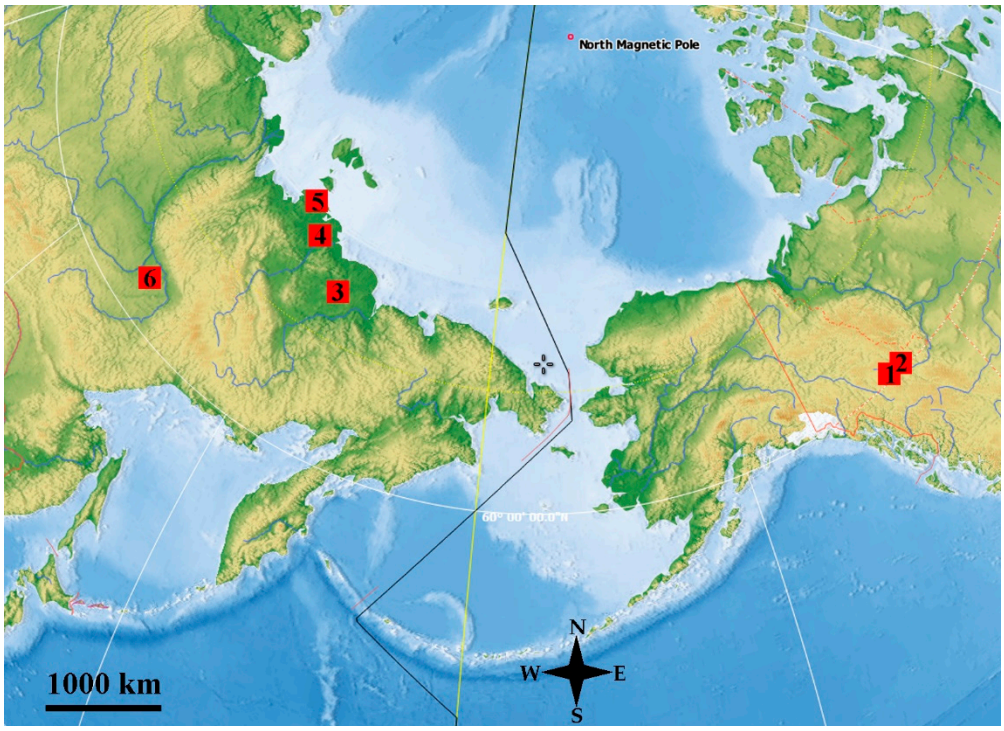


Figure 1. Map of NE Eurasia and NW North America with geographic position of study sites: 1—Tom Creek; 2—Allan Creek; 3—Bol'shaya Chukochya; 4—Staraya Allaikha; 5—Oyogos Yar (Yuka Baby Mammoth); 6—Churapcha. The base map is from the public domain atlas in the desktop app, Marble 2.2.20 (http://edu.kde.org/marble).

CANADA

Yukon Territory:

1. Tom Creek Section. A meander bend of Tom Creek about 5.5 km above its confluence with Liard River (60.2° N, 129.19° W), with organic rich silts underlying Last Glacial Maximum (LGM) till, Late Pleistocene, collected by A. Reyes in 2017; Sample AVR-17TC-9a.

2. Allan Creek Section. North side of the Liard River about 6.5 km below the mouth of Allan Creek (60.49° N, 129.73° W), probably Mio-Pliocene gravels, collected by B. Jensen in 2017; Sample BJ-17 LR-21.

RUSSIA

Republic of Sakha (Yakutia):

3. Bol'shaya Chukochya Mammoth. Middle reaches of the Bol'shaya Chukochya River near Andryushkino village (69.18° N, 154.45° E), Ust-Yansky Ulus: 100+ L of *Mammuthus* sp. hair in alas terrace (a steep-sided depression resulting from thawing of permafrost); various Pleistocene ages; collected by I. Khristenko in late 1990s. The samples are deposited at the Ice Age Museum, Moscow, F-2362/1 [22].

4. Staraya Allaikha Mammoth. Allaikha River near Chokurdah village (70.62° N, 147.92° E), Allaikha Ulus: *Mammuthus* sp. hair in Late Pleistocene yedoma glacial complex deposits of the Kargin Interstadial, various Pleistocene ages (45,000–28,000 cal BP). The samples are deposited at the Ice Age Museum, Moscow, F-4168 [24].

5. Yuka Baby Mammoth Skull. Oyogos Yar locality in the upper third of the north-facing bank of the Kondratievo River (72.68° N, 142.84° E), Ust-Yansky Ulus: mummified *Mammuthus* sp. from hanging melting ledge, composed of loess; radiocarbon date 39,440–38,850 cal BP (GrA-53289), collected in August 2010 by local Yukagir people and then gifted to the Yakutian Academy of Sciences. The samples are deposited at the Academy of Sciences of Sakha (Yakutia) Republic, Yakutsk, accession number OYu-01 [25].

6. Churapcha Rhino. Churapcha settlement (62.00° N, 132.43° E), Churapcha Ulus: woolly rhino (*Coelodonta* sp.) corpse and hair, MIS-2 (19,500 ± 120 cal BP, GIN-9594). The samples are deposited at the Diamond and Precious Metal Geology Institute, Siberian Branch of the Russian Academy of Sciences, IGABM № 2114 [23].

The samples were stored dry since their original collection. Specific details of separating the fossils from the surrounding matrix are presented in the respective publications listed above with each locality. Fossil remains were placed in a small Petri dish and examined in clean water under a Leica MZ7.5 stereomicroscope, and all recognizable branchiopod crustacean fragments were collected using a pipette or forceps and transferred to 96% alcohol. Some branchiopod remains were preliminarily studied with a high power Olympus CX-41 microscope. A portion of the branchiopod remains was air dried, attached to stubs, coated with gold in an S150A Sputter Coater, and studied under a Tescan Vega TS5130MM scanning electron microscope. Individual specimens were identified using relevant literature, references collections, and personal experience.

The stubs for SEM with extracted branchiopods are deposited at the collection of Borissiak Palaeontological Institute of Russian Academy of Sciences (Moscow) as a single total collection, collection number PIN 5670.

3. Results

Figures 2–7.

3.1. Tom Creek

The anostracan eggs (Figure 2a–d) appear very strongly to belong to the chirocephalid genus *Eubranchipus* (Chirocephalidae). This genus is Holarctic in distribution, with all species found in either temperate or subarctic regions. The eggs are most similar to the modern species *Eubranchipus grubii* (Dybowski, 1860) (see Figure 14 in [29] and Figure 6F in [30]), which is currently known from much of Europe and east through Ukraine and central Russia [31]. The eggs bear a slight resemblance to two of the 11 North American species, namely *E. oregonus* Creaser and *E. holmanii* (Ryder) (see Figures 3 and 11 in [32]),

but do not share any overt resemblance to *Eubranchipus* species from eastern Asia (see Figure 8 in [33]). While these eggs are very likely *Eubranchipus*, they either belong to an extinct *Eubranchipus* species or *E. grubii* was at one time much more widespread.

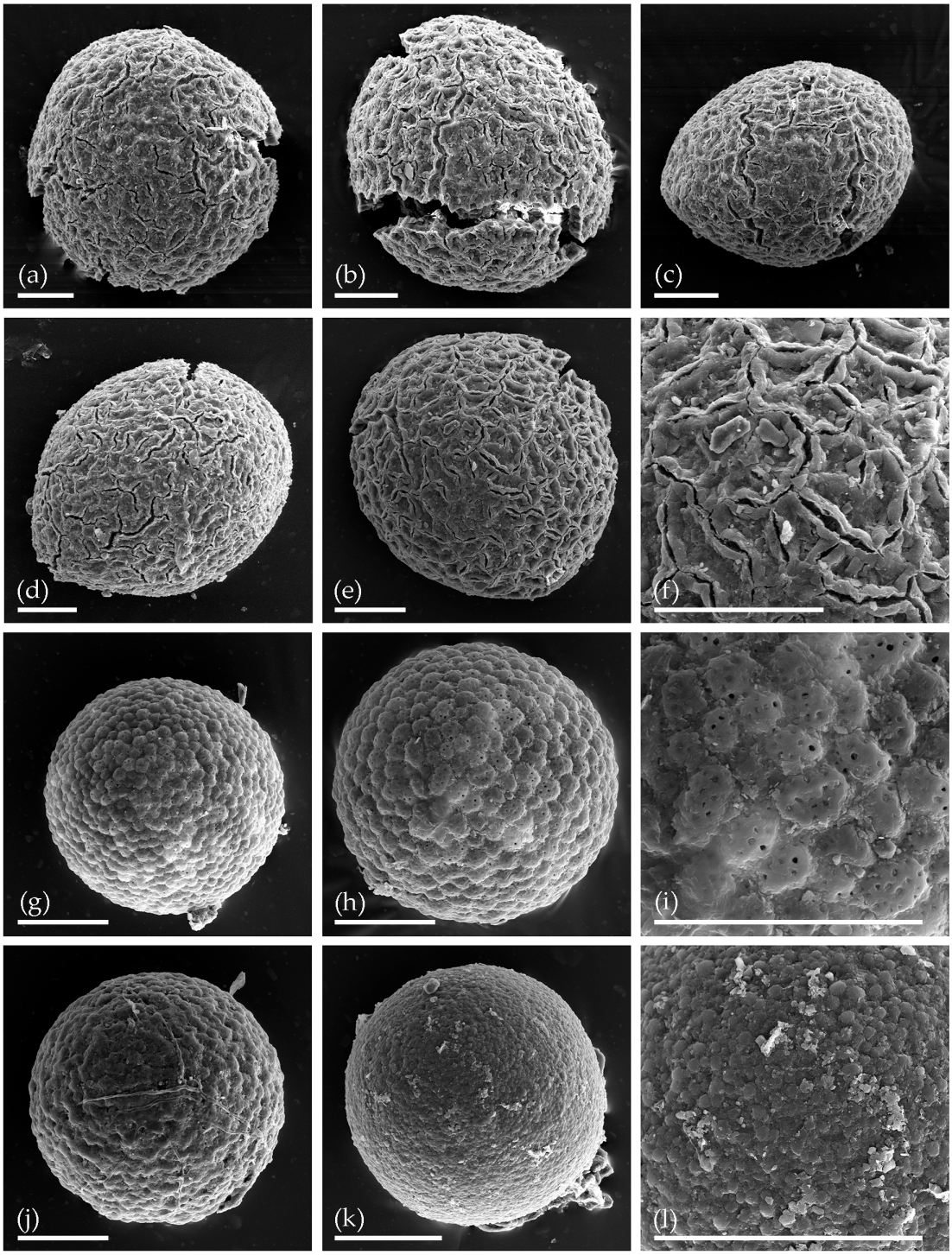


Figure 2. Anostracan eggs. (**a**–**d**) *Eubranchipus* sp., whole eggs from Tom Creek, Canada; (**e**,**f**) *Eubranchipus* sp. from Allan Creek, Canada, whole egg and its detail; (**g**,**h**) *Chirocephalus* sp. from Staraya Allaikha mammoth hair, Russia, whole eggs; (**i**) detail of egg shell in (**h**); (**j**,**k**) whole egg from same locality; (**l**) detail of egg shell in (**k**) Scale bars: 0.1 mm.

3.2. Alan Creek

The anostracan eggs (Figure 2e,f) were identical to those of *Eubranchipus* from Tom Creek.

The single egg (Figure 3c–f) appears to belong to *Branchinecta* (Branchinectidae) (see Figure 4 in [30]); see below.

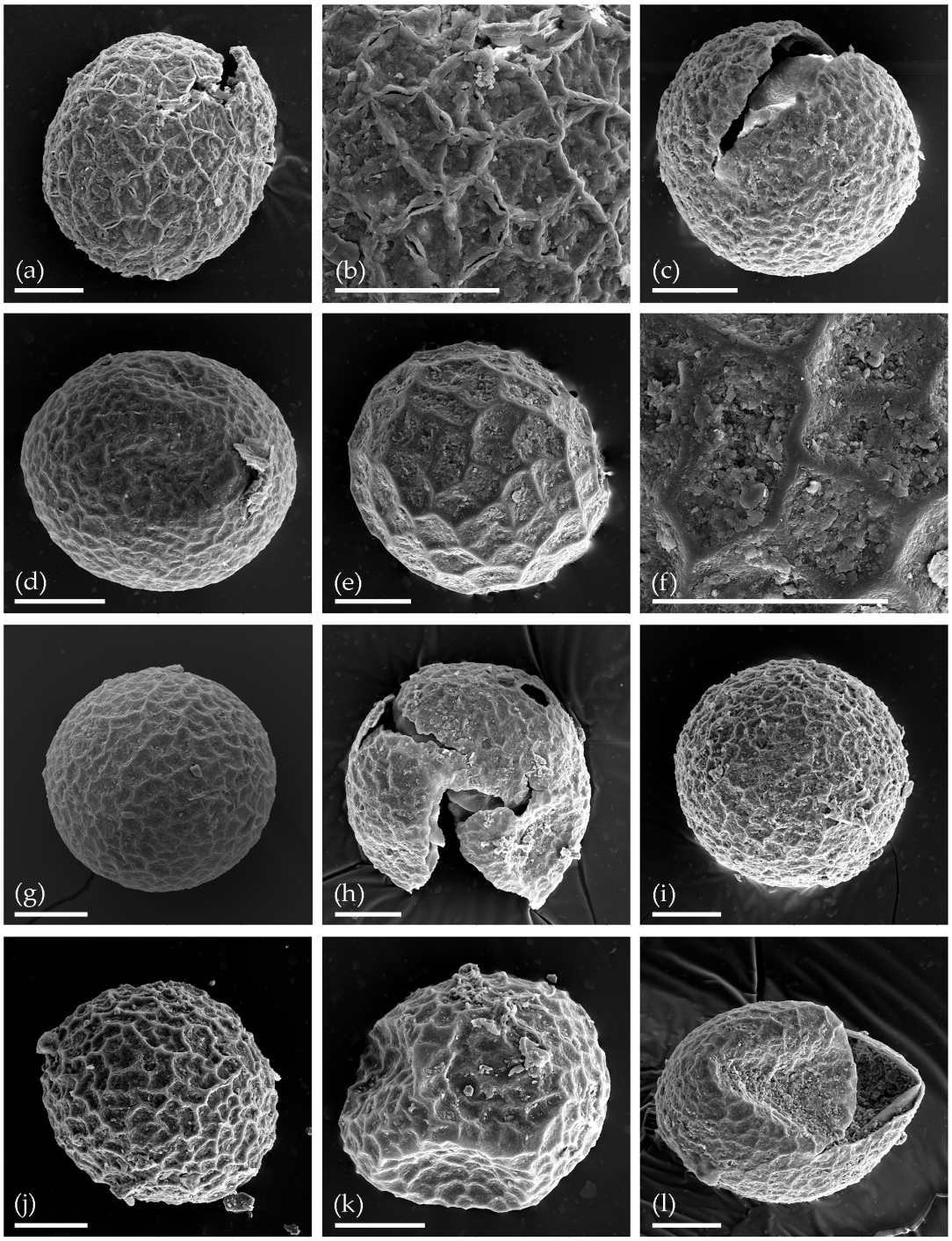


Figure 3. Anostracan eggs: (**a**,**b**) *Branchinecta* sp. from Allan Creek, whole egg and detail of egg shell; (**c**–**e**) *Branchinecta* sp. from Staraya Allaikha mammoth hair, Russia, whole eggs; (**f**) detail of egg shell in **e**. *Branchinecta* sp. from Bol'shaya Chukochya mammoth hair, Russia, whole egg. (**g**–**l**) *Branchinecta* sp. from Yuka baby mammoth skull, Russia, variation in egg forms. Scale bars: 0.1 mm.

3.3. Bol'shaya Chukochya Mammoth Hair

Both anostracan eggs and both anostracan and notostracans mandibles were found enmeshed in the mammoth hair sample. The anostracan eggs represent three separate families. First, Figure 4a shows a single egg that belongs to Branchipodidae, most likely *Branchipus* sp. This genus is currently known from five species, with all but one limited to the western Palearctic. Only the widespread *B. schaefferi* Fischer has a range that extends east into Russia, as far as the Don River.

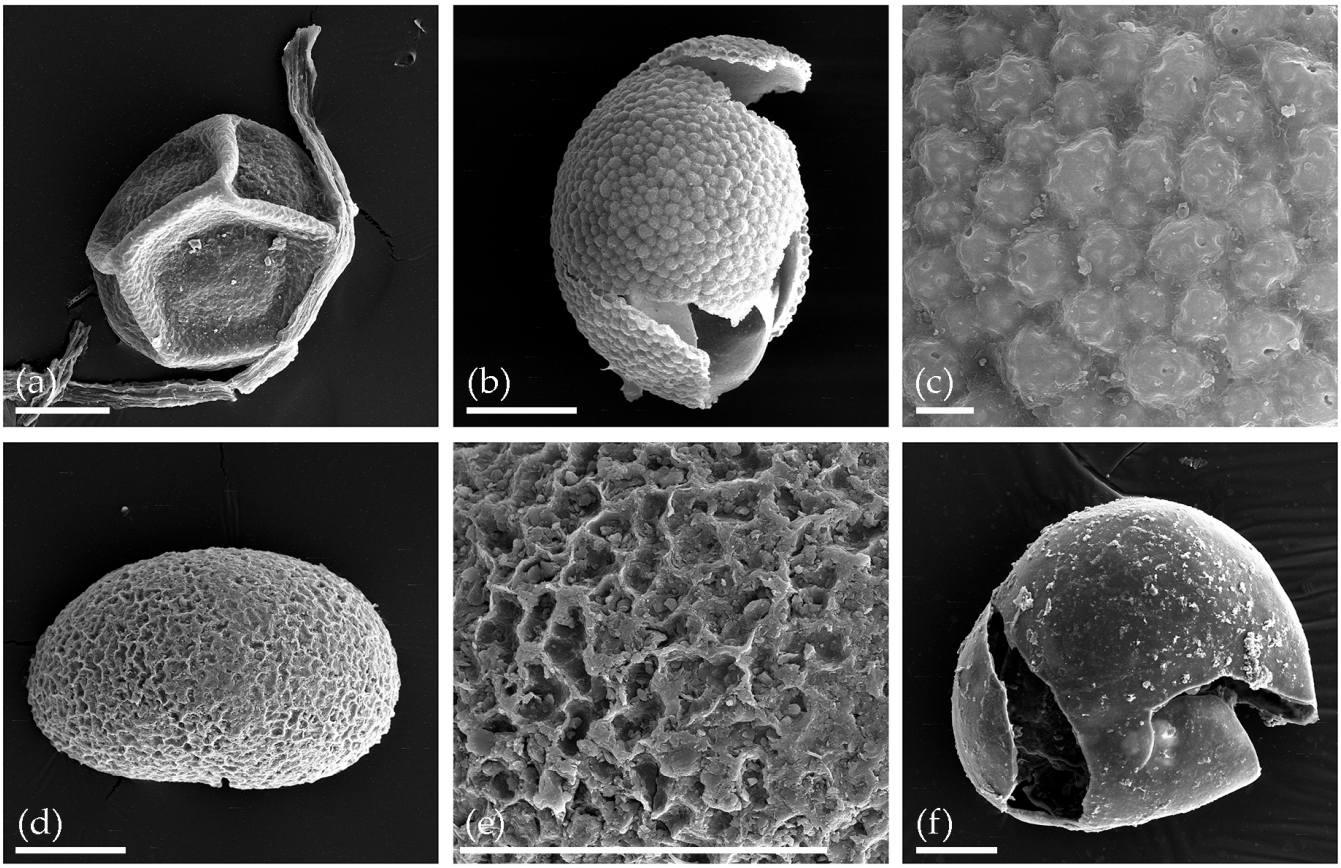


Figure 4. Anostracan and notostracan eggs: (**a**) *Branchipus* sp. from Bol'shaya Chukochya mammoth hair, Russia, whole egg; (**b**) *Chirocephalus* sp., broken egg from same locality; (**c**) detail of egg shell in (**b**); (**d**) potential branchiopod crustacean egg from same locality, whole "egg"; (**e**) detail of shell in (**d**); (**f**) putative notostracan egg from Yuka Baby mammoth skull, Russia. Scale bars: 0.1 mm for (**a**,**b**,**d**–**f**); 0.01 mm for (**c**).

The second anostracan egg appears to belong to Chirocephalidae and appears to belong to the genus *Chirocephalus* (Figure 4b,c).

The next eggs appear to belong to *Branchinecta* (Figure 3g).

The final egg-type item is not clearly a branchiopod egg (Figure 4d,e) but may be a compressed egg from a Chirocephalid or Branchinectid anostracan. It is unclear what it actually represents at this time.

We also recovered anostracan mandibles from this site (Figure 5a–i). These mandibles are lacking certain details necessary for determination; however, they do generally appear to resemble the mandibles of either *Chirocephalus* or *Branchinecta* (see Figure 2 in [34] and Figure 5 in [35]).

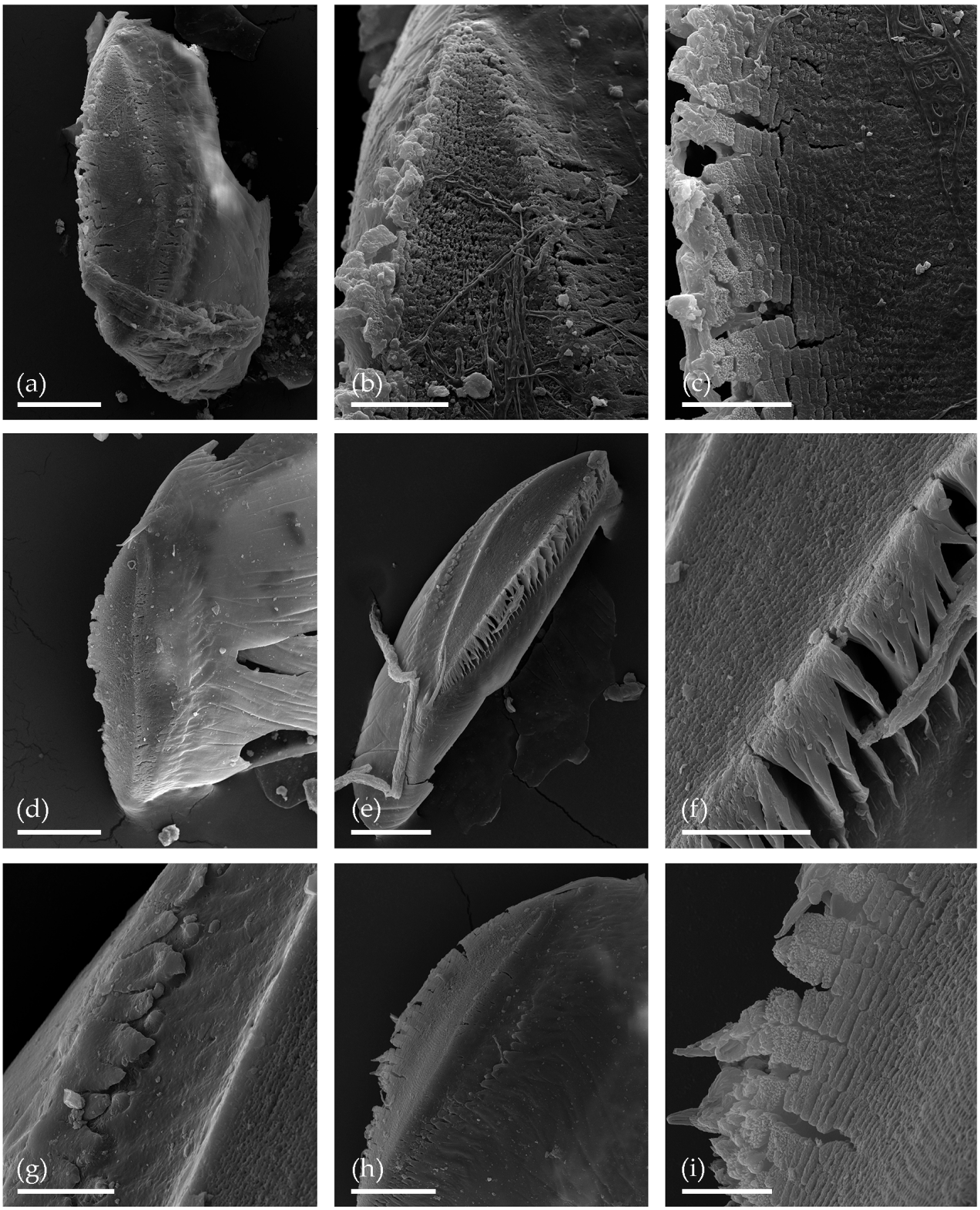


Figure 5. Anostracan mandibles from Bol'shaya Chukochya mammoth hair: (**a**) mandible 1; (**b**,**c**) detail of (**a**); (**d**,**e**) mandibles; (**f**,**g**) details of (**e**); (**h**) mandible; (**i**) detail of (**h**). Scale bars: 0.1 mm for (**a**,**d**–**f**,**g**,**h**); 0.01 mm for (**b**,**c**,**g**,**i**).

The notostracan mandibles (Figure 6i–l) are morphologically similar to species in the genus *Lepidurus*.

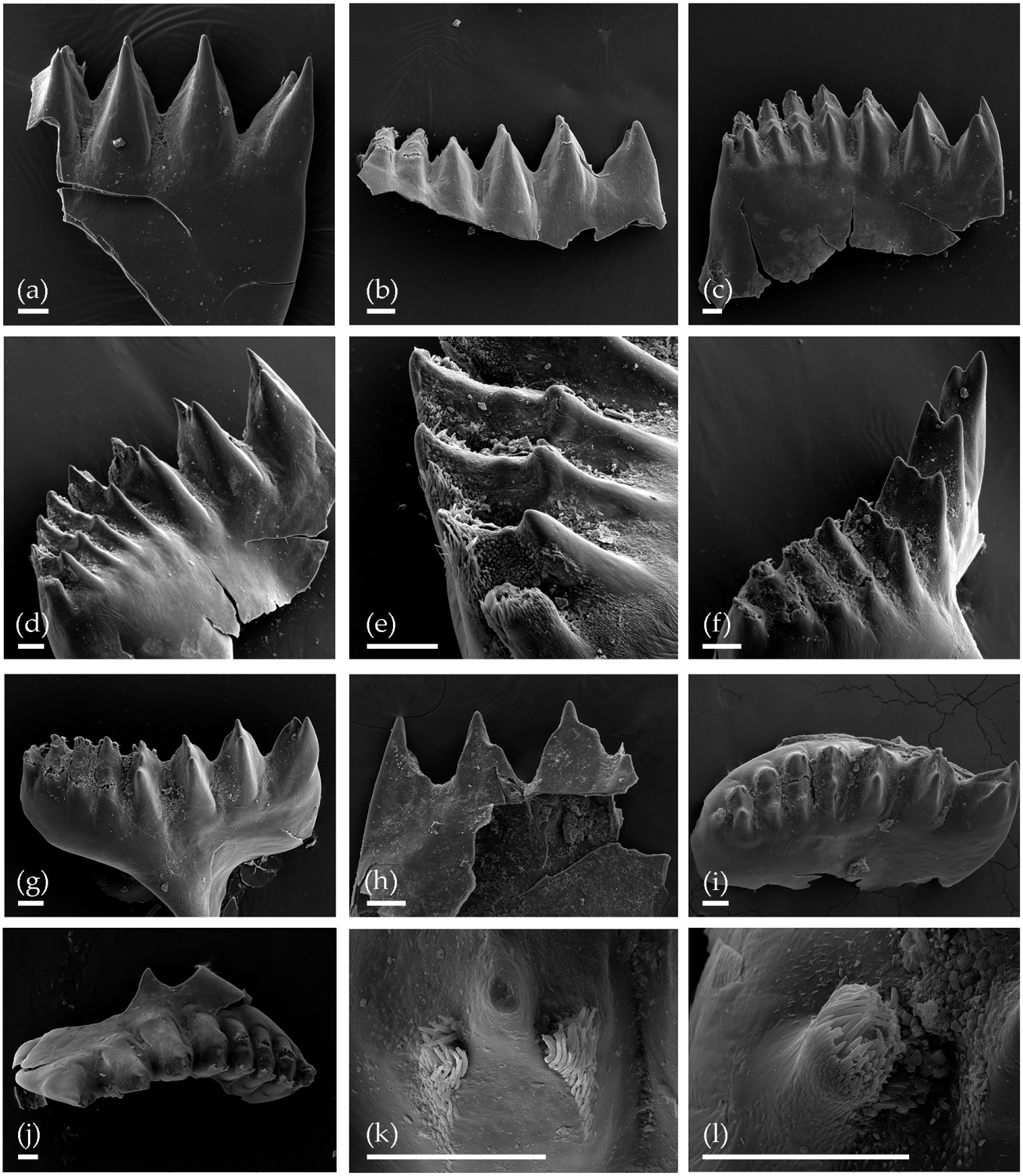


Figure 6. Notostracan mandibles: (**a**–**g**) Staraya Allaikha mammoth hair, Russia; (**h**) Churapcha woolly rhinoceros hair, Russia, mandible fragment; (**i**–**l**) Bol'shaya Chukochya mammoth hair, Russia, mandible crowns (**i**,**j**) and details of I (**k**,**l**). Scale bars: 0.1 mm.

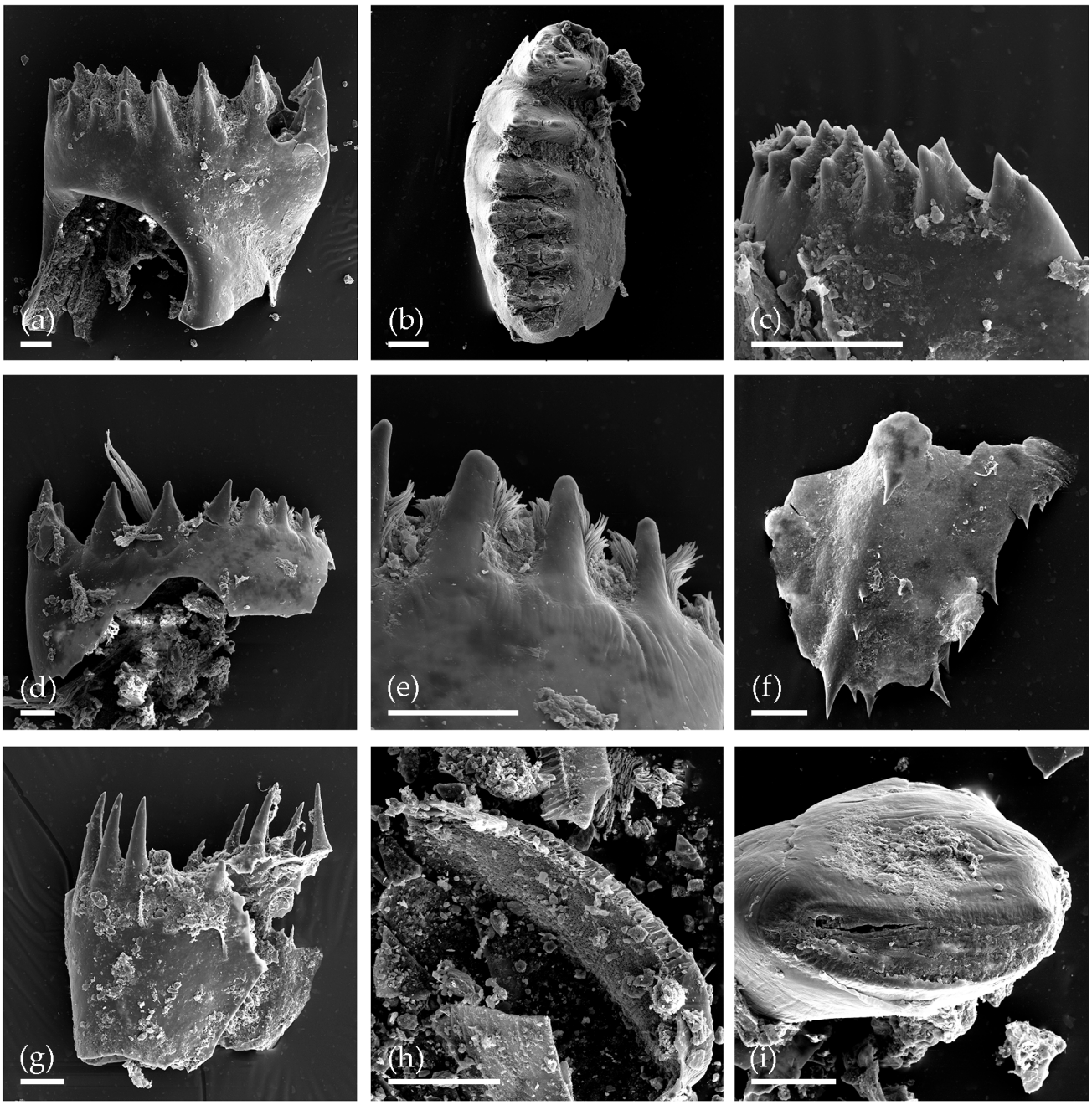


Figure 7. Mandibles and other body portions from Yuka baby mammoth skull, Russia: (**a**) notostracan mandible lateral view; (**b**) notostracan mandible distal view; (**c**) notostracan mandible lateral view; (**d**) notostracan mandible lateral view; (**e**) detail of (**d**); (**f**) notostracan telson fragment; (**g**) possible notostracan maxilla II fragment; (**h**) anostracan mandible; (**i**) anostracan mandible. Scale bars: 0.1 mm.

3.4. Staraya Allaikha Mammoth Hair

The anostracan eggs belong to two different widespread families. Several specimens (Figure 3c–f) appear to belong to *Branchinecta* (Branchinectidae). They are nearly identical to the eggs described above, from Bol'shaya Chukochya mammoth hair. Five or six species occur in Russia, with one (*B. paludosa* (Müller)) being circumpolar in distribution. It is impossible to attribute these eggs to any one species because, with few exceptions, *Branchinecta* eggs are variable not only within species but also within individual egg clutches.

The next eggs (Figure 2g–l) belong to *Chirocephalus* (Chirocephalidae), the second largest genus of extant anostracans [36]. The eggs appears to be identical to the eggs described above, from Bol'shaya Chukochya mammoth hair. The 50+ species in this genus are primarily found in the temperate and subarctic zones of the Palearctic bioregion. These eggs are particularly similar to the extant species *C. chyzeri* (Daday), *C. spinicaudatus* Simon, *C. shadini* (Smirnov), and *C. slovacicus* Brtek (see Figure 9c–g in [30]). The less eroded fossils most closely resemble *C. chyzeri*, a species that is limited to the Slovak Republic and Romania [1]. *Chirocephalus spinicaudatus* and *C. slovacicus* are also limited to Europe; however, *C. shadini* does range from Europe through to northern and central Russia [1]. Our fossils undoubtedly belong to a species that is related to these extant taxa.

The notostracans mandibles (Figure 6a–g) are morphologically similar to species in the genus *Lepidurus*.

3.5. Yuka Baby Mammoth Skull

This skull was found in the remnants of a Pleistocene wetland. Large branchiopod eggs and mouth parts were found on the skull.

Eggs belonging to the anostracan genus *Branchinecta* (Figure 3h–l) were most common and displayed a variety of shell morphologies. These morphologies cannot be ascribed to any recent species. A potential notostracan egg was also recovered (Figure 4f). Notostracan eggs are not discernible between genera or even species. Based on the presence of *Branchinecta* sp. eggs, it can be deduced that the egg may belong to the genus *Lepidurus*, as the two genera typically co-occur together in the northern Holarctic.

Notostracan mandibles were also found (Figure 7a–e). Furthermore, a fragment of a notostracan telson was found (Figure 6f), though not enough is present to determine the genus, as well as a possible distal end of a notostracan maxilla II (Figure 7g).

Anostracan mandibles (Figure 7h–i) were present but with insufficient detail to ascribe them to a genus or family.

3.6. Churapcha Rhino

Only a partial notostracan mandible was recovered (Figure 6h). The mandible most resembles *Lepidurus* sp. Further determination is not possible at this time.

4. Discussion

Large branchiopods are mostly soft bodied animals that very rarely leave any fossil elements behind [4]. Typically, the only fossil remains of anostracans are mandibles [2–4], but occasionally, whole animals are preserved [37]. Notostracans are more common in the fossil record [38] but have mostly been reported as carapaces only [3] and also as ichnotaxa [39]. Clam shrimps, particularly Spinicaudata, are by far the best represented in the large branchiopod fossil record [6,40]; however, they are really only known from their carapaces, and important morphological characteristics of the animal in the carapace are rarely observed [40].

Notostracan mandibles were recorded from the Pleistocene strata only a few times [26]. The eggs and mandibles of fossil anostracans have only recently been explored as a source of paleoecological information [21,25]. This is primarily because no one has spent any time looking for them until recently. Recent large branchiopod eggs and mandibles have been used in extant taxonomy and systematics for decades (e.g., [29,30,32,41,42]).

We found numerous large branchiopod fossil eggs and mandibles in extinct large mammal hair, demonstrating that these mammals wallowed in wetlands, much in the same way that their recent counterparts do today [43,44]. Numerous studies have demonstrated that large branchiopod eggs are passively dispersed unwittingly by mammals, birds, amphibians, and invertebrates (summarized in [14]). However, dispersal to another suitable habitat for the branchiopod is never guaranteed [36]. Hair or other remains from other extinct large mammals should be examined for more large branchiopod fossils (including those stored at museums for a long time [23,24]), although fossils in hair represent multiple

time periods and could not be directly used for reconstructions of the water bodies where they lived [22]. Sediment, dust, or debris should be combed or washed as gently as possible from the mammal specimen, and the sediment should be captured in 0.1-mm sieves. Because most large branchiopod eggs and mandibles are 0.15–0.3 mm in diameter, most branchiopod artefacts should be easily captured in the sieve.

Most large branchiopod artefacts found in our Pleistocene localities belong to taxa inhabiting Holarctic steppe water bodies in recent times, except for the *Branchipus* sp. [21]. It may be that this genus was once more widespread than it is now. Although species-level identifications were not possible for the eggs and mandibles we examined, the differences and variation we observed demonstrate that the genera we did identify have been around at least since the Pleistocene, supporting the idea that there has been a considerable amount of morphological stasis in these animals [4,21,45–48]. Regardless, any and all of these fossils could easily represent taxa that are extant or extinct forms related to modern taxa.

Large branchiopod crustacean species are indicator organisms of seasonally astatic aquatic habitats and/or hypersaline pools and lakes [14,27]. All species live in wetlands with regular wet and dry phases or in hypersaline lakes that may or may not dry up with seasonal regularity. In sediment deposits, the fossils of these animals demonstrate that the paleoecology was a dry climate with regular to sporadic wet seasons. Large branchiopod fossil remains from large mammals demonstrate a similar ecology to what is observed today in the African savannahs: warm to hot, generally dry, with sporadic seasonal wetlands, where large mammals could drink and either wallow to cool themselves or to acquire a mud coating to protect them from biting arthropods (e.g., biting flies and ticks) [43,44]. The presence of these large branchiopod eggs in the hair of these mammals demonstrates that these animals were actively dispersing large branchiopods between wetland habitats and that they may have been important vectors for these crustaceans along migration routes.

Rogers [13,36] demonstrated that different large branchiopod species have very different ecological preferences, each species with its own tolerance range for salinity, cation type and concentration, and % gypsum of the substrate where their pools occur. Thus, these fossils may be indicators of particular geochemical conditions of the water body substrates where the fossils were found or (if gleaned from mammal hair) where the vector had come from to where it was ultimately found.

Therefore, anostracan and notostracan remains are prospective paleoinformation sources, but so far, specific identification is difficult, as the morphology of the fossil resting eggs, mandibles, and telsons from the Beringian region (north eastern Asia and north western North America) does not exactly correspond to recent forms. The main idea of this communication is to attract the attention of paleoecologists to large branchiopod remains, which are quite common in Beringian Pleistocene strata.

Author Contributions: Conceptualization, D.C.R. and A.A.K.; methodology, A.A.Z.; software, A.A.K.; validation, D.C.R. and S.A.K.; formal analysis, A.A.K.; investigation, D.C.R., A.A.Z., A.N.N., S.A.K. and A.A.K.; resources, S.A.K.; data curation, A.A.K.; writing—original draft preparation, D.C.R. and A.A.K.; writing—review and editing, A.A.K. and D.C.R.; visualization, A.N.N.; supervision, D.C.R.; project administration, S.A.K.; funding acquisition, S.A.K. All authors have read and agreed to the published version of the manuscript.

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