

新疆晚三叠世哈萨克虫动物群的进一步研究

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内 容 提 要

新疆上三叠统黄山街组的哈萨克虫是一种已经绝灭了淡水甲壳类, 它与背甲目的淡水蜚虫是形态相似、关系密切、平行演化的两个枝系, 但地质和地理分布远比后者短和局限, 在划分和对比有关陆相地层上十分有意义。过去国内外学者曾对它进行过多次研究, 但对化石本身一些结构构造和形态功能的了解还不十分清楚, 甚或有错误。本文所研究的材料采自吐鲁番、准噶尔和塔里木盆地, 270 块标本上有 400 多个体, 近半数保存有软体印模, 有些标本连胸肢上透明的扇叶的轮廓也由刚毛的痕模压印了出来, 有些标本上还保存有卵粒、食物团、才由肛门排出的粪便以及刚刚孵化出来的幼仔等, 精美绝伦, 堪称化石矿珍藏。通过对这些材料的研究, 发现哈萨克虫有一对远远分开的眼睛长在唇瓣后侧前额的外缘, 背器官下方的圆形凸起不是“一双愈合的复眼”, 而与颞间片上的构造有关; 除第二触角外还有第一触角, 比前者略短; 11 对胸肢的最后两对稍有变化, 其前端的 3 个内肢退化成 2 个, 修正了过去对每个胸肢结构构造认识上的错误, 找到了鳃副叶与扇叶的正确位置。记述了淡水蜚虫与哈萨克虫的区别, 阐明了后者的生活习性, 并对其个体发育、肌肉系统、血液与脱氧的关系、生存古环境等方面的问题进行了讨论和探索。

关键词 哈萨克虫 晚三叠世 新疆

A FURTHER RESEARCH INTO LATE TRIASSIC
KAZACHARTHRA FAUNA FROM XINJIANG UYGUR
AUTONOMOUS REGION, NW CHINAChen Pei-ji¹⁾, K·G·McKenzie²⁾ and Zhou Han-zhong³⁾

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Key words Kazacharthra Fauna, Late Triassic, Xinjiang

INTRODUCTION

Malacostracan crustacean fossils with well-preserved soft parts, such as crabs, and

shrimps, are not uncommon in the geological record but the discovery of well-preserved soft anatomies of lower Crustacea is infrequent and always excites interest among carcinologists. The Kazacharthra are an extinct crustacean group, fossils of which were found for the first time in Kazakhstan (Chernyshev, 1940) but they received scant attention until Novojilov (1957, 1959) published details of their soft anatomy, including a description of the structure of the thoracic limbs, which confirmed a relationship with the notostracan Branchiopoda (Tasch, 1969). The horizon yielding these striking fossils was dated by the two Russian writers as Lower Jurassic.

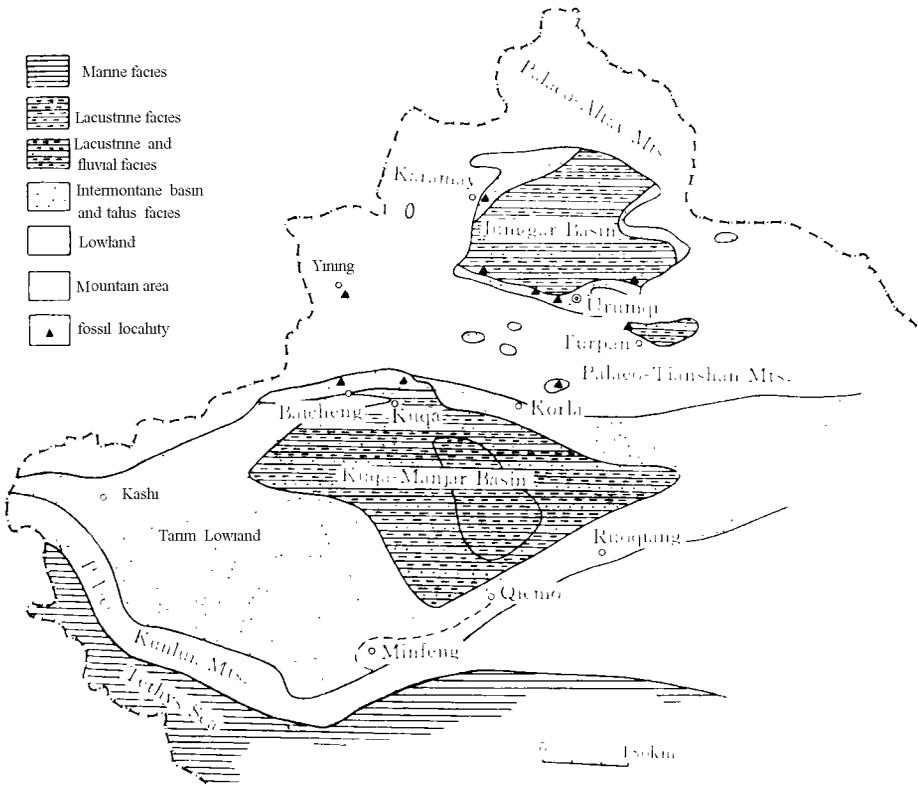
In 1965, while engaged in coal prospecting work, Mr. Zhou Han-zhong collected some kazacharthran specimens from the Keerjian District of Toksun County on the western margin of the Turpan Basin in Xinjiang Uygur Autonomous Region. These samples, which were identified by Prof. Zhang Wen-tang as *Almatium*, occurred in association with the well-known Yenchang flora of Late Triassic age.

During the 12th Annual Conference of the Palaeontological Society of China held in Suzhou near Shanghai in 1979, Mr. Zhou Han-zhong presented Prof. Hong You-chong with some specimens from his collection which Hong later reported as a new genus, *Xinjiangiops* (Hong 1980) — an unavailable name because it is preoccupied by *Almatium* (Chen and Zhou, 1985). Since then, many more kazacharthran fossils, of *Almatium*, *Panacanthocaris* and *Jeanrogerium* in particular, have been found in the Keerjian District by Mr. Zhou Han-zhong and a further collection was made there by Chen Pei-ji and Zhou Han-zhong in 1983.

In recent years, numerous new kazacharthran localities have been reported from Xinjiang (the Junggar, Turpan, Yanji and Tarim Basins; Yining area) and SW Mongolia (Text-fig. 1). As a result, the known kazacharthran fauna now comprises around 25 species in 9 genera. The respective stratigraphic horizons have been carefully correlated and are dated as late Middle Triassic to Late Triassic in age (Compiling Group of the Regional Stratigraphic Chart of Xinjiang, 1981; Wei, 1984; Badamgarav, 1985; Chen and Zhou, 1985). Among these materials, the *Almatium* specimens from the Keerjian District are far better preserved than Novojilov's collections from Kazakhstan and rank with the most spectacular fossils ever recorded. In a short paper, McKenzie, Chen and Majoran (1991) provided a redescription based on some of the new specimens, with additional discussion on shield shapes and speculation on the possible reproductive modes of *Almatium gusevi* (Chernyshev, 1940).

LOCATION AND STRATIGRAPHIC POSITION

So far, we have 270 rock specimens with Kazacharthra from three localities in the Turpan, Tarim and Junggar Basins respectively.

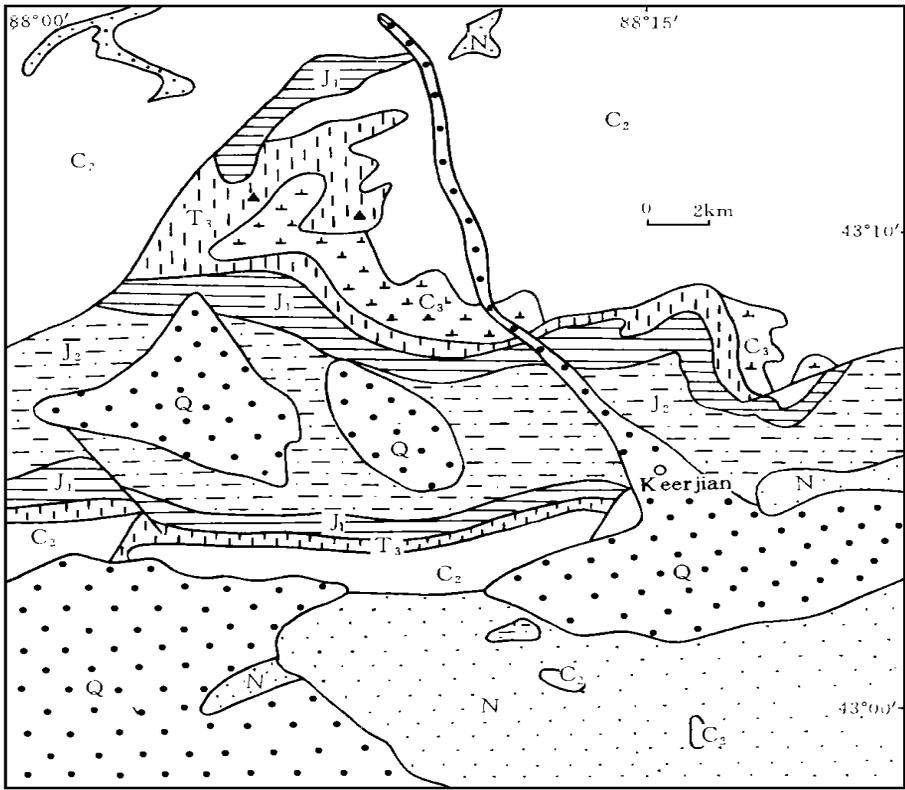


Text-fig. 1 Sketch map showing Late Triassic palaeogeography and the known localities for kazacharthran fossils in Xinjiang

A. Keerjian District, western margin of the Turpan Basin

In Keerjian, 50km NW of Toksun town, the Upper Triassic deposits are well exposed and referred to the Huangshanjie Formation which lies unconformably above Carboniferous volcano-sedimentary rocks (Text-fig. 2). The Huangshanjie Formation is a nonmarine facies and can be divided into four units in descending order as follows:

4. Greyish fine-grained sandstone, sandy mudstone and mudstone in alternating beds, with plant macrofossils of *Danaeopsis* sp., *Bernouillia* sp., *Neocalamites* sp.; the palynomorphs *Punctatisporites* sp. and disaccitate pollens; palaeoniscid fish remains; the conchostracan *Mesolimnadiopsis* sp.; plus the kazacharthrans *Almatium gusevi*, *A. n. sp. (?)*, *Panacanthocaris ketmenica* Novojilov, 1957 and *Jeanrogerium sornavi* Novojilov, 1959. 234m
3. Yellowish-green coarse-grained sandstone, becoming medium-grained sandstone eastward and sandy conglomerate westward. 83m
2. Grey argillaceous siltstone, with sandstone and purplish-red mudstone towards the base and greyish-black carbonaceous shale in the upper part; with the plants *Danaeopsis fecunda* Halle, *Bernouillia zeilleri* Pan, *Neocalamites carcinoides*, *Equisetes sarrani*, *Cladophlebis* sp.; palaeoniscid fish remains; and an indeterminate mollusc species. 43m



Text-fig.2 Geological map and kazacharthran fossil localities of the western Turpan Basin, Xinjiang

Q = Quaternary; N = Neogene; J₂ = mid-Jurassic Xishanyao Fm.; J₁ = Lower Jurassic Badaowan and Sangonghe Fms.; T₃ = Upper Triassic Huangshanjie Fm.; C₃ = Upper Carboniferous volcanic rocks; C₂ = Mid-Carboniferous flysch facies clastics.

- 1. Greyish-green, purple and other variegated colour conglomerates. 15m
- unconformity —————

underlying Carboniferous volcano-sedimentary rocks.

B. Karamay, western margin of the Junggar Basin

The late Middle Triassic to Upper Triassic Xiaoquagou Group is distributed in strips along the piedmont, northwest of Karamay city. Its stratigraphic sequence, from top to bottom, is as follows:

Upper Triassic Haojiagou Formation (12.99m)

- 5. Greyish-green or greyish-black mudstone and siltstone, with cross-bedding and coaly streaks. 2.71m
- 4. Black carbonaceous mudstone alternating with greyish-black mudstone. 1.03m
- 3. Greyish-green or greyish-brown siltstone, fine-grained sandstone, sandy mudstone and mudstone, with laminations and coaly streaks, yielding plant macrofossils of *Thinnfeldia norden*.

- skioldi*. 3.79m
2. Greyish-black sandy mudstone, greyish-green siltstone and fine-grained sandstone in alternating beds, with cross-bedding and thin coaly streaks. 4.48m
1. Greyish-brown and greyish-green argillaceous siltstone and fine-grained sandstone, with laminations and interspersed coaly streaks. 0.98m

————— conformity —————

Huangshanjie Formation (36.0m)

5. Yellowish-grey silty mudstone, changing to siltstone with pea gravels downward, yielding the kazacharthran *Jeanrogerium sornavi* and homopteran insects. 4.4m
4. Greyish-yellow mudstone with quartz sand and pea gravels, bearing fossil kazacharthrans and plant fragments. 2.4m
3. Yellowish-grey silty mudstone with ferruginous nodules in the lower part, yielding abundant kazacharthran fossils in the upper part. 13.9m
2. Yellow mudstone with spathic iron in the top part, carrying abundant kazacharthran and plant fossils. 7.1m
1. Yellowish or yellowish-grey silty mudstone with spathic iron, yielding the fossil plants *Todites shensiensis* and *Equisetes* sp. 8.2m

————— conformity —————

lower Upper Triassic Karamay Formation (69.1m)

7. Dark grey mudstone with grains of ferruginous oolite, capped by 0.1m of yellowish-white clay. 1.4m
6. Yellowish and greyish-green sandy mudstone and sandstone with ferruginous oolitic grains, yielding the fossil plants *Neocalamites damularioides* and *Danaeopsis fecunda*. 6.8m
5. Greyish-green mudstone and siltstone with dark brownish-red mudstone and intercalations of ferruginous fine-grained sandstone, yielding the fossil plants *Neocalamites hoerensis* (Schimper) Halle, *Equisetites* sp., *Protoblechum hughesi* and *Danaeopsis fecunda*. 5.7m
4. Brownish-red and yellowish-green coarse-grained sandstone and siltstone in alternating beds, containing the fossil plants *Chiophleris? yuani*, *Thinnfeldia nordenskioldi*, *Glossophyllum? shensiensis*, *Sphenopteris* sp. and *Todites cf. shensiensis*. 19.7m
3. Greyish mudstone changing eastward to dark purplish mudstone. 1.0m
2. Dark brownish-red, yellowish or greyish-green mudstone, sandy conglomerate and conglomerate in alternating beds, with the fossil plants *Thinnfeldia nordenskioldi*, *Todites cf. shensiensis*, *Sphenobaiera cf. crassinervis*, *Equisetites* sp. and *Taeniopteris* sp. 21.6m
1. Yellowish-green conglomerate associated with grey thin-bedded sandy mudstone, carrying in the top part the plant fossils *Taeniopteris* sp. and *Neocalamites cf. carrerei* Zeiller. 12.9m

————— unconformity —————

underlying Upper Palaeozoic volcanic rocks.

The Karamay Formation in this district also carries the fossil plants *Lepidopteris otto-*
nis, *Cladophlebis cf. paralobifolia*, *Phlebopteris* sp., *Bernouillia zeilleri*; the
kazacharthrans *Almatium gusevi* and *Zhungarium* spp.; the insects *Triassoblatta*
fudupinensis, *Lacocorixia divena*, *Ademosynoides minor*; the conchostracan *Mesolimna-*

diopsis? sp.; palaeoniscid fish; and the bivalves *Ferganoconcha sibirica*, *F. rotunda*, *Tutuella karamaiensis*, *Sibiriconcha sitnikovae* and *S. anodontoides*.

c. Kuqa-Baicheng area, northern margin of the Tarim Basin

The Upper Triassic rocks are exposed mainly in the Kuqa-Baicheng area, on the northern margin of the Tarim Basin. They can be divided into the Huangshanjie Formation below and the Tariqiye Formation above. For the latter, the geological age is undecided between Late Triassic (determined on sporopollen) and Early Jurassic (based on plant macrofossils and conchostracans). In descending order, the stratigraphic sequence is as follows:

Upper Triassic or Lower Jurassic Tariqiye Formation (821m)

3. Greyish-white to greyish-brown sandy conglomerate, feldspathic debris sandstone and medium- to fine-grained greywacke intercalated with greyish-brown mudstone, silty mudstone, greyish-black carbonaceous mudstone and coal seams, bearing fossil macroplants, sporopollen and conchostracans. 301m
2. Greyish-black to greyish-brown mudstone and silty mudstone intercalated with grey to brownish-grey marl and thin-bedded siltstone or calcareous nodule beds, containing fossil sporopollen. 443m
1. Grey to greyish-green sandstone and conglomerate in the lower part; and unequally thick interbeddings of grey to brownish-grey fine-grained greywacke, fine-grained calcareous debris sandstone, siltstone and grey to greyish-yellow mudstone or silty mudstone in the middle to upper parts, carrying fossil sporopollen. 77m

————— disconformity —————

Upper Triassic Huangshanjie Formation (298m)

7. Greyish, greyish-white or greyish-green thick-bedded quartzose sandstone and fine-grained sandstone, with thin-bedded conglomerate. 109m
6. Greyish-green siltstone. 10m
5. Black carbonaceous shale and greyish-green coarse-grained sandstone, bearing plant and kazacharthran fossils. 15m
4. Greyish-green siltstone, intercalated with fine-grained sandstone, containing plant fossils. 23m
3. Greyish-black mudstone, with plant fossils. 12m
2. Greyish-green medium- to thick-bedded sandstone intercalated with grey feldspathic sandstone and dark greyish-green argillaceous siltstone. 81m
1. Greyish-green conglomerate, sandy conglomerate and coarse-grained feldspathic-quartzose sandstone, intercalated with greyish-green sandstone. 48m

————— unconformity —————

lower Middle Triassic sandstone or pre-Cambrian rocks.

The Tariqiye Formation is a coal-bearing series, containing such typical Early Jurassic plant and conchostracan fossils as: *Neocalamites nathorsti* Erdtmann, *Cladophlebis* sp., *Sphenobaiera* cf. *spectabilis* (Nathorst) Florin, *Czekanowskia?* sp., *Podozamites bullus*

Wu and Zhou, *Strobolites* sp.; and *Palaeolimnadia* cf. *chuanbeiensis* Shen from the upper part of the Kuqa River section. The sporopollen assemblage, on the other hand, occurs throughout the Tariqiike Formation and is very uniform. The principal taxa are *Ara-trisporites granulatus* (Klaus) Playford and Dettmann, *A. fischeri* (Klaus) Playford and Dettmann, *Cyathidites minor* Couper, *Punctatisporites* sp., *Dictyophyllitites harrisii* Couper, *Concavisporites toralis* (Leschik) Nilsson, *Angiopteridospora* cf. *denticulata* Chang, *Osmundacidites wellmanii* Couper, *Apiculatisporites* sp., *Lophotriletes* sp., *Lycopodiacidites regulatus* (Couper) Schulz, *Duplexisporites scanicus* (Nilsson) Playford and Dettmann, *D. gyratus* Playford and Dettmann, *Annulisporea* sp., *Psophosphaera* sp., *Chasmatisporites hians* Nilsson, *Classopollis annulatus* (Verb.) Li, *Ginkocycadophytus nitidus* (Balme) de Jersey, *Pseudowalchia* sp., *Taeniaesporites alberta* Jansonius, *Prototraploxylinus* sp., *Oudraeculina anellaeformis* (Bolch), Pocock, etc. They can be correlated with sporopollen of the Haojiagou Formation in the Junggar Basin and the Yenchang Formation in the Ordos Basin and indicate a Late Triassic age (Wu and Chen, 1990).

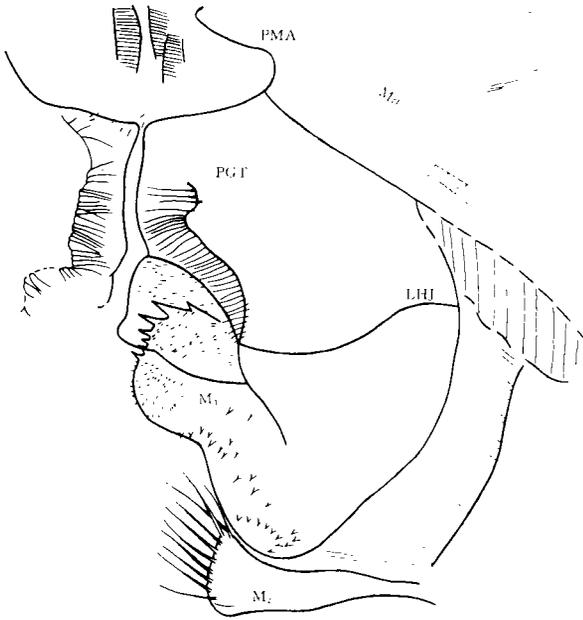
The Huangshanjie Formation of the Kuqa-Baicheng area yields kazacharthran, plant and sporopollen fossils. Of these, the kazacharthrans include *Almatium gusevi*, *Kungeja* cf. *tchakabaevi* Novojilov, 1957 and *Ketmenia kugaensis* Wei, 1984. The reliably determined macroflora consists of only one species, *Neocalamites hoerensis*, collected by Wu Shun-qing and Zhou Han-zhong in 1984.

Sporopollen fossils of the Huangshanjie Formation at this locality include *Punctatisporites triangularis* Ouyang, *Dictyophyllum harrisii*, *Concavisporites toralis*, *Apiculatisporites* sp., *Lophotriletes* sp., *Osmundacidites* sp., *Duplexisporites scanicus*, *D. gyratus*, *Psophosphaera* sp., *Abietineaepollenites pectinella* (Mal.) Liu, *Ara-trisporites granulatus*, *Cordaitina* sp., *Pityosporites divulgatus* (Bolch.) Pocock, *Annulisporea* sp., *Parataeniaesporites pseudostratus* (Kapytova) Liu, *Podocarpidites multesimus* (Bolch.) Pocock and *P. multicimus* (Bolch.) Pocock. This assemblage may be correlated with the palynoassemblages of the Huangshanjie Formation in the Junggar Basin and the Yenchang Formation in the Ordos Basin and is undoubtedly Late Triassic in age.

In recent years, a consensus appears to have been reached with Russian and Mongolian workers that the kazacharthran deposits are Late Triassic in age. Thus, in a floristic analysis, Dobruskina (1980) correlated the Triassic sediments of southwestern Mongolia with the Madigen, Ketman and Bashki floras of Russia which were previously considered to be Early Jurassic but are now regarded as Ladinian-Carnian in age. These Mongolian deposits also carry the kazacharthran *Almatium gobiense* (Badamgarav, 1985).

NEW DATA ON *ALMATIUM GUSEVI*

Our possession of abundant new well-preserved materials has provided the basis for developing a much more detailed understanding of the Kazacharthra, in particular *Al-*



Text-fig. 3 110800. The maxillule and maxilla RHS, $\times 25$

PMA = location of postmandibular apodemes, Md = mandible

LHJ = lateral hinge joint; PGT = paragnath

M₁ = maxillule, M₂ = maxilla

matium gusevi which is by far the most commonly occurring kazacharthran available to us. Study of these materials has led to the discovery of more new data on which we report briefly herein. We have also taken the opportunity to refer to and dissect specimens of two living Australian Notostraca (*Triops australiensis* and *Lepidurus viridis*) which have enabled a closer comparison between Notostraca and Kazacharthra than we had made in previous reports (Chen and Zhou, 1985; McKenzie, Chen and Majoran, 1991).

Prior to commencing our re-examination of *Almatium gusevi*, we recognised that our specimens were preserved in four different ways: as dorsal (pl. VI, fig. 1) or ventral (p. I, fig. 1) animals; and dorsal or ventral casts. This was crucial to analysing the parameters of *Almatium* correctly.

The headshield of *Almatium gusevi* is frequently the only part of the animal which is preserved, although it was obviously rather thin as shown by the many specimens in which it is wrinkled or crumpled. [We now concur with an earlier referee's opinion that what we thought might have been a venous network in the headshield is an effect of such crumpling (McKenzie, Chen and Majoran, 1991, p. 310)]. The entire dorsal surface of the headshield was covered with low, small rounded pustules (K 510), mostly almost flush with the surface but in places more prominent, including the mid-posterior margin; and it ap-

pears to have been micropunctate everywhere except medially. We can add that, along the anterior margin particularly, the ornament also consisted of fine and close-set striations (p1. II, figs. 1-2). The marginal doublure was thickened almost uniformly along the whole periphery of the headshield, except in front and ventrally where it became much broader and linked to the front of the head. As argued previously, the headshield was convex upwards and lacked a vertical midline (unlike *Notostraca*). New data which confirm its convexity include the fact that the notch has different depths even in specimens which have the same headshield width and length; this suggests that originally convex headshields were differentially flattened during *post mortem* compression. The margin of the notch itself and the posterior headshield margin on each side of it had numerous small marginal denticles (K406).

In dorsal animals, at about $1/3$ of the length of the headshield from the front, there were symmetrically opposed and well defined mandibular humps with single linear ridges below them — similar features characterise notostracans, e.g. *Triops australiensis*. We call these linear ridges the thoracic yoke (p1. II, fig. 6); it served to define the boundary between the cephalic and thoracic limbs, even when no limbs were fossilised. Of the two rounded projections along the median plane which we discussed earlier, the posterior one is typically located below the trace of the mandibles in non-distorted fossils. We are certain that this is the impression of the two maxillular pads facing each other, i.e., it is an artefact of *post mortem* compression by overlying sediment. The anterior rounded projection was definitely not a housing for fused compound eyes as suggested by Novojilov (1960); this will become apparent anon. However, we remain uncertain about the correct interpretation for this feature, which is typically located just above the mandibular coxae, although we are inclined to believe that it was a type of dorsal organ.

The front of the head had a broad W-shape distally (p1. II, fig. 1) and was marginally thickened. On each side, at about the region where the broad anteromarginal doublure linked to it, there was a lateral eye, with perhaps a suture line to the doublure from it (p1. II, figs. 1, 2). On one particularly good large specimen, the lateral eye on the left hand side in a ventral animal seems to have two compartments (the right hand side is not so well preserved). In the light of this discovery, and although we have over a dozen specimens which show these lateral eyes, as might be expected, the preservation is rarely ideal; we are certain that the two symmetrical slits in the front of the head, which we earlier interpreted as probable loci for compound eyes, in fact are eye slit pores (p1. II, fig. 3) each of which led to the water sac covering its respective lateral eye and also, presumably, to the nauplius eye (Calman, 1909, fig. 29). Occasionally, fine fibrils leading from a lateral eye towards its eye slit pore are also preserved. Other newfound structures associated with the front of the head are trusses (p1. II, fig. 4). There were two of these, one on each side fitting approximately into the distal bulge of each lobe of the broad ventral W-

shape. Each truss was subtriangular, with the base inwards and the apex reaching to about the lateral eye region; also, each truss incorporated a smaller similar triangle at its apical end. Functionally, these trusses strengthened the front of the head in the area where the labrum was 'hinged' to it. We note here that in an earlier contribution (McKenzie, Chen and Majoran, 1991) the front of the head was called the labrum, and the flap below it was termed the labium. In this paper, however, we adopt the terminology of Fryer (1988).

The kazacharthran labrum (formerly termed labium by us) was relatively small, but its size in proportion to the front of head and headshield generally was about the same as in living Notostraca (cf. Fryer, 1988, figs. 1, 63). Its shape was flap-like, and the distal margin had a relatively broad flange (p¹. II, fig. 5). In some specimens, impressions of the two central longitudinal muscles which attached the inner face of the labrum to the inner front of the head are clearly preserved.

We have several additional fossils which show the large shell gland of the kazacharthran headshield, including at least one individual in which both shell glands can be clearly seen (p¹. II, fig. 6). In an earlier contribution (McKenzie, Chen and Majoran, 1991), the occurrence of a shell gland was held to be presumptive evidence for the presence of a maxilla. We now have direct evidence for the presence of a maxilla, as will appear shortly, but have not yet identified the excretory tube of the shell gland in the proximal maxillar region, although we have no doubt that it was located there in all Kazacharthra.

Kazacharthra had a full set of cephalic limbs. As noted earlier, the paired antennules were uniramous and located on either side of the head (p¹. III, figs. 1, 2). We can add that their attachment sites were probably a little below but near the lateral eyes. Each antennule was multi-segmented and comprised up to 15 segments; on occasional specimens only 11–12 segments could be confidently identified. The tip probably carried a few fine, short, sensory hairs.

The abundant new materials enable us to correct an earlier error with respect to the kazacharthran antenna (McKenzie, Chen and Majoran, 1991, p. 310). We have many specimens which clearly display the kazacharthran antennae but these show them to have been relatively small, *vis-a-vis* the antennules, as well as uniramous and unisegmented. We are now certain that the multi-segmented antennal exopod which we referred to earlier was a displaced antennule that unfortunately was preserved in such a position as to make for confusion with an antenna. On many of the new specimens, both antennules and antennae are clearly visible. The antennules are the outer pair and the antennae are the inner pair (p¹. III, fig. 3). This indicates that the antennae were located lower on the kazacharthran cephalon, i. e., nearer to the mandibles than the antennules. Because of their position inside of the antennules, we briefly considered that they might represent

paired frontal sense organs, such as those in larval *Triops cancriformis* (Claus, 1873, Pls. 6–8), but rejected this idea for some cogent reasons. Firstly, we have several fairly well preserved larval stages of *Almatium gusevi* and none of these show any trace of frontal sense organs; secondly, they should be located much nearer to the midpoint of the frontal margin and also typically project beyond it (they are not and do not); and thirdly, they appear to be too large in comparison with the frontal organs of larval Notostraca.

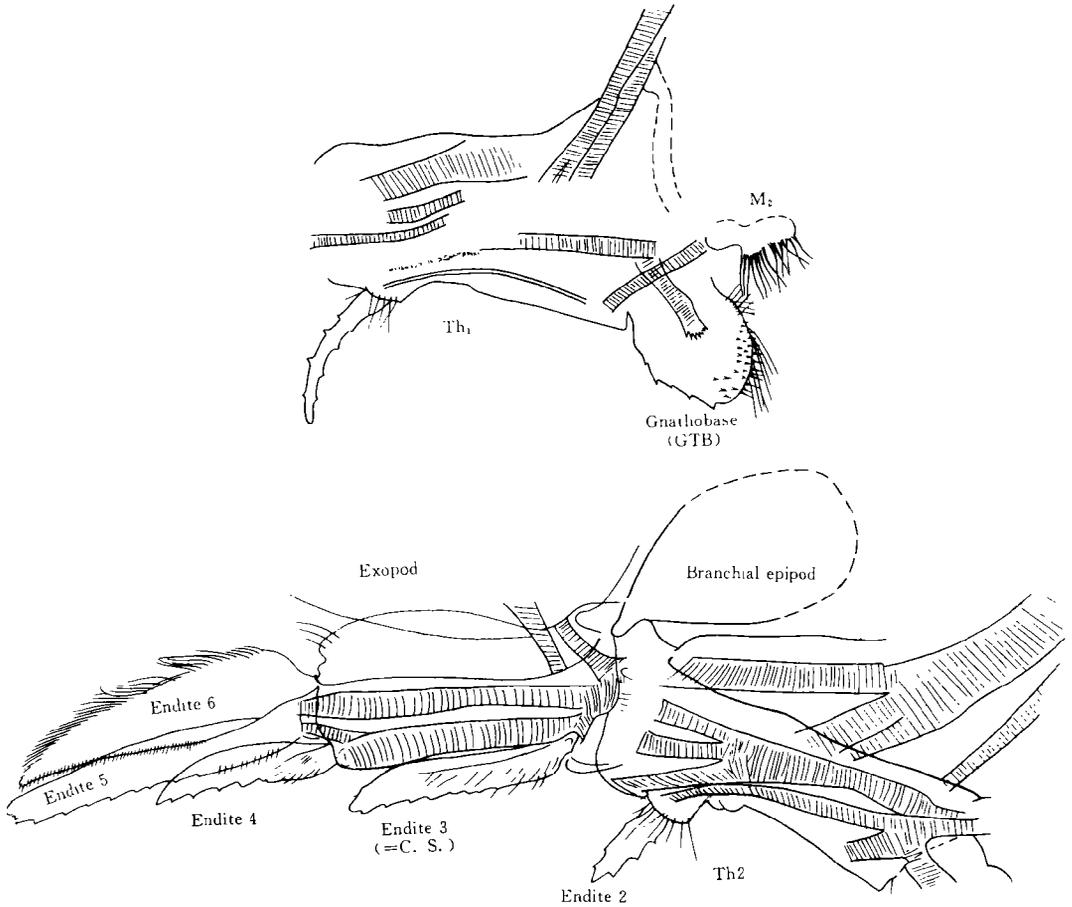
The kazacharthran mandibles (McKenzie, Chen and Majoran, 1991, p. 311) were large, extremely powerful and very well muscled, with a large posterior cavity (p1. III, fig. 4). Their shape and dentition also are reminiscent of notostracan mandibles and, as is typical for Crustacea (Manton, 1969), they were modified coxae. In adult kazacharthrans, as in adult living notostracans, the mandibular coxae comprised this entire limb. Our new data on the kazacharthran mandibles relate mainly to their musculature and will be discussed later in that section.

We are indebted to the monograph by Fryer (1988) on the Notostraca, as well as to the availability of fortunately preserved specimens, for our understanding of the remaining kazacharthran cephalic limbs. The paired paragnaths were located immediately behind the mandibles (K 439). As in Notostraca, they were robust features which joined to the maxillules at the postmandibular apodemes. Their shape was subcrescentic. Along the upper inner margin each paragnath had a fringe of long hairs projecting inwards and at the lower tip it had a bushel of fine spiky hairs. In life, the kazacharthran paragnaths would have been mostly covered by the equally robust but more complex maxillules which were sited behind them. The maxillules united with the paragnaths at the postmandibular apodemes and along the lateral hinge joint; in this region there was also a cup-like structure which must have housed the abductor muscle, as in Notostraca (Fryer, 1988, fig. 100). The total armature of each maxillule was complex and differentiated. It comprised a lobe of powerful teeth, a pad covered with minute denticles, and an area bearing numerous relatively longer spiny hairs (Text-fig. 1). The positional relationship of each of these subarmatures to the others seems very similar to the situation in Notostraca (Fryer, 1988, p1. 3, figs. 44, 45). The minutely denticulate opposing pads could touch each other. This fact, together with the robustness of the kazacharthran maxillules, created the impression of a rounded projection in dorsal animal fossils, as noted above in our discussion of the head-shield.

The final cephalic limb in Kazacharthra was the maxilla. This limb is less frequently preserved in our material, although we have half a dozen specimens, because it was relatively weak and hidden between the large maxillules and the powerful first thoracic limbs. As in Notostraca (Fryer, 1988, p. 75), the kazacharthran maxilla was relatively small and simple. It comprised a flattened lobe armed distally with longish spiny hairs (Text-fig. 3), which proximally became narrower and folded on itself. As noted earlier, we could not

trace it further proximally to the point where the excretory duct of the shell gland became united with it, although we had dissected material of *Triops australiensis* (in which this excretory tube is flattened short and quite stout) available for comparison and thus knew where to look.

The thorax of adult *Almatium gusevi* carried 11 paired limbs; of these the eleventh limb in mature females bore the egg masses in modified exopods of that limb as notostracans do (Fryer, 1988, fig. 10). We have yet to discover definite male reproductive structures in kazacharthran fossils.



Text-fig. 4 Australian Museum p11328. Thoracic limb (Th₁ and Th₂) structure of a small ovigerous female of *Triops australiensis* (headshield width about 17mm); ×16

It took a dissection of living *Triops australiensis* to make us fully aware of the relationships of the various elements of the kazacharthran thoracic limb to each other and to the limb as a whole (Text-fig. 4). In life, the thoracic limb of *Triops* is oriented so that endite 1, which is a gnathobase, faces inwards to the food groove, while the exopod and

branchial epipod are dorsal, endites 2 and 3 are ventral, and endites 4–6 are terminal (Claus, 1873, p1. 8, fig. 8; Fryer, 1988, figs. 9–15). The kazacharthran thoracic limb as illustrated by Novojilov (1959, fig. 2, p1. 8, fig. 6) clearly fits this pattern but is inaccurate in its detail as well as incomplete. His praecoxa is obviously our gnathobase (cf. Fryer, 1988, figs. 5–15), but missing altogether in Novojilov (cit., fig. 2) is the branchial epipod and this led to considerable confusion for us. We eventually located it on our best specimen (a ventral animal), exactly where it should be, inwards of and alongside the exopod (Text-fig. 5; p1. IV, figs. 1, 2). We had missed it earlier, because in this specimen the thoracic limbs were preserved upside down, i.e., what had been dorsal in life was ventral when the ventrally preserved animal was squashed flat during *post mortem* compression. Once located, we were able to confirm that the branchial epipod occurred on at least the first 8 thoracic limbs and we have no doubt that it was present on all 11. We also realised that Novojilov (cit., fig. 2) had misidentified endite 3 as a praeepipodite, because it had become detached and was out of place on his best specimen; and that he had misidentified endite 2 as an epipod because the true (branchial) epipod was not seen by him. We found that endite 2 was a small setose lobe located at about the mid-coxale and that it occurred on all the thoracic limbs (Text-fig. 6). The kazacharthran endite 3 was an elongate setose lobe which issued from the ventral junction of the coxale and corm [we use the term corm for the basipodite of Novojilov (1959, p. 266)]. Novojilov's carpopodite is homologous with the endopod (=endite 4) of living Notostraca (cf. Fryer, 1988). It was coarsely setulose dorsally and with the propodite (=endite 5 of Notostraca) also occurred on all kazacharthran thoracic limbs. However, we found Novojilov's dactylopodite (=endite 6 of Notostraca) only on the first 9 thoracic limbs; it appears to have been lost on limbs 10 and 11 (p1. III, fig. 2). Finally, the kazacharthran exopod was a large setose appendage which occurred dorsally on all 11 thoracic limbs (Text-fig. 5; p1. IV, fig. 1). Ventrally, along the middle of the entire thorax ran a shallow food groove (Text-fig. 6, p1. I, fig. 1) — we were mistaken earlier (McKenzie, Chen and Majoran, 1991) in thinking that one did not occur.

Posterior of the kazacharthran thorax came the abdomen. The first two or three segments of the abdomen were genital segments; they also carried gnathobase-like structures which presumably were similarly functional as the true (thoracic) gnathobases — in some individuals these structures also occurred on the first two or three abdominal segments which carried dorsal nodes (Text-fig. 7). We have searched the genital segments carefully in all the many specimens which show the upper abdomen without being able to identify gonopores or other sex characters. The remainder of the abdomen in mature forms consisted of 24–28 segments ornamented with paired lateral segments and dorsal nodes. Thus the maximum number of abdominal segments was 31 (not 33 as we reported earlier). Between two segments was a section of flexible tissue which enabled considerable flexure by



Text-fig. 5 848402. The branchial epipods and other features of the thoracic limbs, preserved upside down relative to their life position; $\times 10$

the animals in life. We can add, to the details of the abdominal ornament previously noted by us, such as the double row of dorsal nodes and the lateral marginal spines carried by each segment, that in well-preserved individuals each abdominal segment was covered by numerous minute spinulose hairs.

The telson and caudal spines were described by McKenzie, Chen and Majoran (1991). Many new telson specimens also display the paired circular ducts we described then (p¹. VI, fig. 2); these are surely homologous to the similar features mentioned for the first time in Notostraca by Linder (1952). Further, the kazacharthran telson had three short spines around the anal opening which was located terminally, one on each side with the third medial and above. The caudal rami were adorned, especially proximally, with very numerous, tiny and fine spinules or spinulose hairs. In good specimens this ornament seems to have been tiered (p¹. VI, figs. 2, 3).

Previously we recorded the total length of a large adult (headshield width about 47 mm) as around 90–95 mm (McKenzie, Chen and Majoran, 1991). When we consider the largest mandible in our material (K 205, over 6 mm long), the total length of the individual to which it belonged must have approached 150 mm.

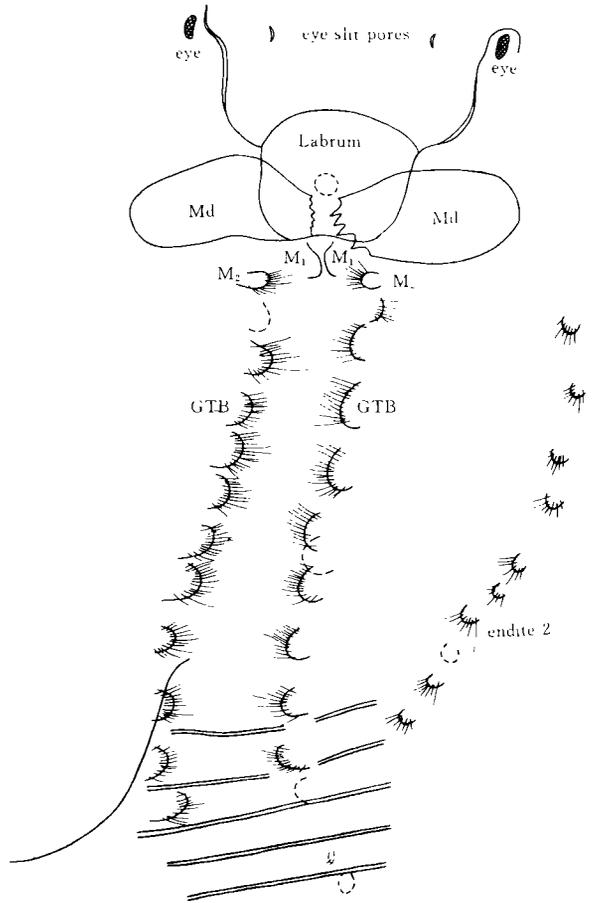
OTHER SPECIES

In addition to *Almatium gusevi*, we consider that there may be at least one other species of *Almatium* in our material (K 460, pl. VI, fig. 5). The samples also contain many specimens of *Panacanthocaris ketmenica* and *Jeanrogerium sornavi*, plus a few individuals each of *Iliella* sp., *Kysyltamiopsis* sp. and *Ketmenia* sp.

DIFFERENCES BETWEEN
KAZACHARTHRA AND
NOTOSTRACA

While closely related to Notostraca, Kazacharthra are sufficiently different to be regarded as an equivalent group evolved from some common as yet undetermined ancestor. In the headshield, the main difference is the absence of a vertical midline in Kazacharthra and its presence in Notostraca. Further, the Kazacharthra had widely-separated ventrally-borne lateral eyes unlike the close-set and dorsally-housed compound notostracan eyes. Importantly, the kazacharthran antennule was multi-segmented, whereas the notostracan antennule is unisegmented; and although the kazacharthran antenna was small it was still much more prominent than the vestigial antenna which is hard to find on Notostraca. The mouth parts in both groups are so closely similar that we regard them as the definitive synapomorphic character for these two orders.

The thoracic limbs of Kazacharthra were clearly dissimilar in detail to those of Notostraca, although their basic structural homology is undoubted. Thus, kazacharthran thoracic limbs were not as obviously phyllopodan as in the Notostraca; and all of endites 2-6 are distinctly different between these two groups, as our discussion above and reference to Fryer (1988) have made it clear. As we will discuss later, kazacharthran egg masses contained far more eggs than, for example, the 5-20 per laying period reported for young



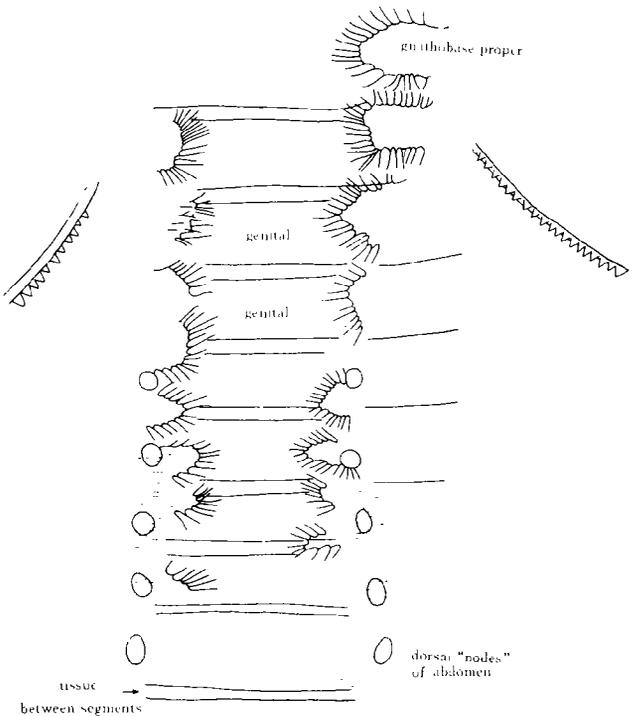
Text-fig. 6 110805. The shallow food groove, endite 1 (gnathobases) and endite 2 (small setose lobes) of the thoracic limb on the RHS of a ventral animal; $\times 10$

adult females of *Triops orientalis* (Karande and Inamdar, 1959). Even the smallest ovigerous female in our material carried more than 20 eggs in each brood pouch, and the larger animals were so heavy with eggs that, in one remarkable specimen (p1. VI, figs. 3, 4) which must have died when about to shed its brood, they were spread over 9 abdominal segments.

There were no abdominal limbs in the Kazacharthra. Perhaps, the gnathobase-like structures on the genital and uppermost 2-3 dorsally nodose abdominal segments represent relicts of abdominal limbs (Text-fig. 7). And the maximal number of abdominal segments was fewer in kazacharthrans than it is in living Notostraca. Finally, the supra-anal plate of the telson in Kazacharthra was quite different to that of the notostracan *Lepidurus* (we had comparative material of *Lepidurus viridis* available).

A NOTE ON BRANCHIOPOD PHYLOGENY

Walossek (1993, fig. 41) has recently published a new interpretation of presumed relationships within Branchiopoda, together with his selection of major synapomorphic characters of the presumed monophyletic units. Our discovery of ventral, separated lateral eyes in Kazacharthra (p1. II, figs. 1, 2), means that his synapomorphies 4 (internalisation of compound eyes and shifting of them toward the dorsal surface) and 5 (protrusion of forehead region including the compound eyes during ontogeny) need reevaluation. Nevertheless, we concur with Walossek (cit.) that Kazacharthra and Notostraca are sister groups with a natural association in Calmanostraca and suggest that the highly characteristic chewing-biting mouthparts of Calmanostraca, versus the more variable but mainly grinding-rolling mouthparts of anostracans are preferable synapomorphic characters to separate Sarsostraca and *Rehbachella* from Calmanostraca. The rather striking differences between



Text-fig. 7 K 406. The abdomen of a large individual, showing "gnathobases" on genital segments and on the first 3 noded segments; $\times 16$

the two orders of Calmanostraca as summarised above justify, in our opinion, the erection of this supraordinal category to accommodate them. Our position on branchiopod heterogeneity, therefore, differs from that of Fryer (1987). Consideration of the phylogenetic relationship of the calmanostracans, including Kazacharthra, to conchostracans and cladocerans (as these are commonly understood) is beyond the scope of this paper.

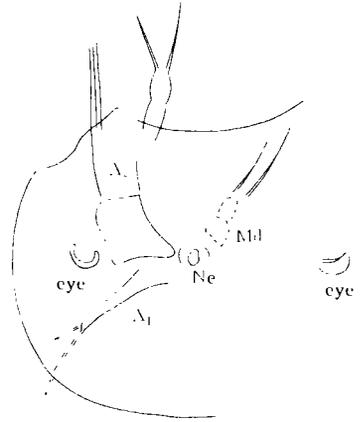
ONTOGENY

There are several main constraints upon attempting to outline the ontogeny of any small fossil. These include: even smaller larval stages; a more delicate soft anatomy, and greater susceptibility to damage or displacement or to minor variations in texture of the generally clay- or silt-sized host sediment. With regard to Kazacharthra, some other factors also apply. Firstly, their larval forms were probably a preferred prey for the larger animals (see the "Habits of Life" section); and secondly, their hitherto unknown ontogeny had some novel features which made our task much more difficult. Fortunately, the ontogeny of species in the nearly-related Notostraca is well known and our attempt has been considerably assisted by reference particularly to Claus (1873) and Fryer (1988).

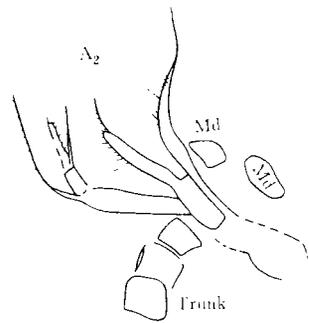
Adult female Kazacharthra carried their eggs in a pair of brood pouches, one on each side of the 11th thoracic segment. Even in the smallest ovigerous female, there were masses of eggs in each pouch. This is not the case with young mature females of *Triops* as reported by Karande and Inamdar (1959) and confirmed by us following dissection of several young females of *T. australiensis* (and *Lepidurus viridis*). When shed, the eggs appear to have been released en masse not separately as illustrated by Fryer (1988, fig. 4). Several such shed egg masses occur in our material (p1. VI, figs. 3, 4). The maximum egg size we measured was about 0.45mm (specimen 110800).

The first stage after hatching was by far the most numerous. Many slabs are literally packed with them but all were obviously very soft and have crumpled to such an extent that it is impossible as yet to discern any structure apart from a broadly oval shape. Their size was around 1 mm.

We have only one example of a form that we consider to have been the second larval



Text-fig. 8 81840a. The presumed second larval stage, not well preserved; $\times 16$
 A_1 = antennule A_2 = antenna
 Ne = nauplius eye



Text-fig. 9 K 456. A displaced, broad and branched antenna, mandibles and several trunk segments of the presumed third larval stage; $\times 25$

stage of *Almatium gusevi*. It was found on the same slab as our best specimen (84840a). The partially preserved headshield had a width of about 2.95 mm and a height of around 3 mm, but no ornamentation. The soft anatomy was characterised by two prominent, widely separated eyes, a convex medial hump which we think housed the nauplius eye, a simple unsegmented antennule, a broad and branched antenna and, possibly, a 2-3 segmented mandible endopod (Text-fig. 8). This is quite different from the second larval stage of *Triops cancriformis* as illustrated by Claus (1873, p. 1. 6) in which, although the headshield has a roughly similar shape, there are no lateral eyes and the nauplius eye and cephalic limbs occur well towards the front of the animal not centrally as in our example. Thus, the kazacharthran lateral eyes did not appear late in their ontogeny but were present very early, giving emphasis to our earlier comments on phylogeny.

There are several specimens of what we regard as the third larval stage. Again, the separated lateral eyes were prominent (on the best example, likewise associated with 84840a), there was a central nauplius eye, a rudimentary front of the head and a fairly well preserved branched antenna. The headshield on this and other specimens of the stage was very finely striated (cf. Claus, 1873). The antenna is preserved in greater detail on K 456. It had a large protopod from the coxa of which issued a long, strong and highly setose bristle; at the end of the basale, the limb branched into a weaker 3-4 segmented endopod with fine setules and a stronger exopod which carried a long dorsodistal bristle on its first segment and shorter setae on its 2-3 (possibly) remaining segments. K 456 also shows 2 small mandibular coxae. The most distinctive feature of this stage, however, was the trunk which had 5 rounded segments followed by a telson segment with 2 rather thick and short caudal rami. There were also many exopodite lobes (K 453, K 456) showing that several thoracic limbs or their Anlagen, at least 5, were developed by this stage (Text-fig. 9; p. 1. V, figs. 4, 5).

There is no material of the fourth and later early larval stages. We believe that the best explanation for this was that they were prey for larger kazacharthrans. But there are several examples of subadult juveniles. From studying these it seems as if they represent more than a single species of *Almatium* as we indicate below.

K 498 is a headshield of 11.5 mm width, having the typical *Almatium* shape with marginal denticles in the notch region which is quite deep (about 2.5 mm). This animal had a large multisegmented and setose antenna, a small dorsal organ, broad mandibular coxae with a serrated distal edge, maxillules represented by two pads touching medially, a well developed thoracic yoke and humps for the mandibular muscles, plus the indication of many exopodites in the thoracic region. No abdomen is preserved on this specimen but we believe that the same stage is represented by several examples on K 506, ranging in size from about 9-11 mm. The headshield shape is similar and at least one appears to have a large antenna; another shows the mandibles, maxillules and thoracic yoke. The abdomen

in a third individual consists of 12 segments with short paired lateral spines (one each side). Its telson (1 mm wide by 1.5 mm high) has numerous small lateral spines (10–12 a side), 2 more prominent terminal spines around the base of each caudal spine, and also shows the longitudinal telson muscles and a supra anal flap. The caudal spines are missing (p1. V, fig. 2).

A smaller *Almatium* individual (K 442, width 9.5 mm, notch 1.5 mm) nevertheless seems more advanced. There was a dorsal organ and thoracic yoke, plus (displaced on this specimen) both mandible coxae, and a labrum with the adult shape. The abdomen comprised 18 abdominal segments with long paired lateral spines (one each side), plus 2 genital? segments. The telson was distinctly wider relative to its height (width 2.2 mm, height 2.5 mm) than in adults and carried several lateral spines. The caudal spines were considerably flexed and about 4 mm long (p1. VI, fig. 5). Another specimen representing this stage (K 515) has a similar-sized headshield displaying mandibles, labrum and lateral eyes; the front of head was about 1.5 mm wide.

K 212 is the incomplete abdomen of another juvenile individual. It shows that the lateral spines of some young *A. gusevi* were remarkably long and powerful.

There are at least two more juvenile *Almatium*, K 444 and K 499. The headshield is about 19 mm wide in the larger of the two (K 499) which has 19 abdominal segments with large lateral spines. K 444 has a total of 21 abdominal segments and the front of head measures 6.5 mm (pl. VI, fig. 1).

K 460, with a headshield width of around 15 mm is the smallest ovigerous female in our collection. It had the full complement of adult limbs described earlier⁻⁹ of the exopodite lobes are beautifully detailed on the RHS⁻ and also bore a dorsal organ. The front of head was about 3 mm wide. The numerous eggs were carried in paired brood pouches of the 11th thoracic segment. The abdomen (incomplete) had long lateral spines (p1. VI, fig. 6). K 500, with a headshield width of about 12.5 mm, is another example of the same taxon. The front of head was about 3.5 mm wide and it had over 20 abdominal segments carrying large lateral spines. We think that these two individuals may represent a different species of *Almatium* from *A. gusevi*.

The smallest ovigerous females of undoubted *A. gusevi* have a headshield width of about 25 mm, which lies in the most common size range of all our adult material. Our largest ovigerous female had a headshield width of 44 mm.

MUSCULATURE

The excellent preservation of the abundant material available to us has led to some unexpected and novel dividends with regard to kazacharthran musculature. We were fortunate in having the available monograph of Hessler (1964) on cephalocarid skeletomusculature, which carries a long section on comparative crustacean skeletomusculature, as well

as the recent work by Fryer (1988) on Notostraca.

The kazacharthran headshield by homology with other branchiopods was an expansion of the dorsal cuticle and as such might be expected to be devoid of musculature. However, Fryer (1988) illustrates a cephalic bracing tendon which occurs on "each side, and not far from the midline" of the head. There is no clear evidence as yet for such tendons in Kazacharthra which, however, as we noted above, bore triangular trusses on either side of the "midline" that must have braced the head (p¹. II, fig. 4). Functionally, these trusses would have been advantageous in several other ways. Firstly, in the vertical plane, they widened the head behind its anterior margin, thus making the front more efficient for burrowing and grubbing into the bottom mud. Secondly, they would have provided a base against which the midgut wall anchored (Fryer, 1988, p. 55-56, fig. 63). Thirdly, and just as importantly, they would have created an anteriorraum for the tubules of the digestive gland (by homology with Notostraca) in the lower part and for the lateral eyes and their associated water sacs in the upper part. For the latter function, the small similar triangle at the apical end of each truss would have provided extra support and protection. We have already referred to the presence of fibrils in the eye regions.

The flap-like labrum had several sets of associated muscles (p¹. V, fig. 1). One, located on each side at its proximal part, attached that flank of the labrum to the front of the head. The usefulness of locating these muscles, which are clearly displayed on many specimens, is that they indicated the anterior commencement of the oesophagus (cf. Fryer, fig. 63). Further, as we noted above, there were at least two large longitudinal muscles which connected the inner face of the central part of the labrum to the inner front of the head. With such a musculature, the labrum was clearly capable of some adductor-abductor movement.

Neither the extrinsic nor any intrinsic musculature of the antennules and antennae has been identified by us as yet. Both of these limbs were rather weak and the function of the antennae is difficult to envisage. On the other hand, the presence of small terminal hairs at the ends of some antennules and their multisegmented character indicate that there must have been some associated musculature and that their function was probably sensory.

The mandibular coxae were heavily muscled, as they are in the Notostraca. Apart from many thick intrinsic transverse bands of muscle (K 464), prominent extrinsic muscles ensured that kazacharthran mandibles were capable of limited but forceful promotor-remotor as well as abductor-adductor movements, making them efficient biter-chewers; there must also have been several strong suspensor muscles (Fryer, 1988, figs. 66, 67). The transverse mandibular tendon is particularly well preserved on one large individual (K 502). It was thick, with stout ligaments at each end.

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