

Phyllocarid crustaceans from the Middle Ordovician Šárka Formation at Praha-Vokovice

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Abstract. A phyllocarid assemblage is described from the lower part of the Šárka Formation of Praha – Červený vrch Hill. *Caryocaris subula* Chlupáč, 1970 prevails whereas *Caryocaris wrighti* Salter, 1863 is much less frequent. The definition of *Caryocaris* published by Racheboeuf et al. (2000) is followed. The mode of life and occurrence of *Caryocaris* is also discussed in this paper.

Key words: phyllocarid crustaceans, Ordovician, Šárka Formation, Barrandian

Introduction

The shales of the Šárka Formation exposed in a temporary excavation near Červený vrch Hill at Praha-Vokovice are exceptionally rich in phyllocarid crustaceans represented by genus *Caryocaris*. The phyllocarids overwhelmingly dominate the fossil assemblages (see Kraft et al. 2003, this volume).

Results

Although the material collected from the Červený vrch Hill is comparable with that described by Chlupáč (1970) from other localities, the unusual abundance of *Caryocaris* at this locality and its mode of occurrence deserve attention.

Superclass Crustacea Pennant, 1777

Class Malacostraca Latreille, 1806

Subclass Phyllocarida Packard, 1879

Order Archaeostraca Claus, 1888

Family Caryocarididae Racheboeuf, Vannier et Ortega, 2000

Genus *Caryocaris* Salter, 1863

Comments: The diagnosis of the widely distributed genus *Caryocaris* was first proposed by Rolfe in the Treatise volume (1969), by Chlupáč (1970), Jell (1980) and recently in somewhat emended form by Racheboeuf et al. (2000). An important contribution to the general knowledge of the genus was made by Churkin (1966) who stressed several particular features of *Caryocaris* (e.g. composition and enrollment of the carapace valves). Chlupáč (1970) subdivided the genus into two subgenera, namely *Caryocaris* (*Caryocaris*) Salter, 1863 and *Caryocaris* (*Rhinopterocaris*) Chapman, 1903 – originally classified by Chapman as a separate genus based on the type species *R. maccoyi* Chapman, 1903 from the Ordovician of Victoria, Australia. The main difference between *Caryocaris* (*Caryocaris*) and *C.* (*Rhinopterocaris*) is the

presence of an anterodorsal carapace projection (horn) in the latter. Other taxonomical problems were discussed by Jell (1980) who concluded that uncertain generic assignment of the types of *Rhinopterocaris* Chapman, 1903 and its relation to *Caryocaris* were uncertain. According to Racheboeuf et al. (2000) the subdivision between the two subgenera is not necessary due to the presence of transitional forms between *Caryocaris* (*Caryocaris*) and *C.* (*Rhinopterocaris*) (sensu Chlupáč 1970).

Caryocaris Salter, 1863 is a very distinctive genus whose morphology (particularly the posterior denticulate margin, configuration of telson and furcal rami) and carapace structure (resistant and flexible cuticle) have well-defined characteristics. Its separate position as a representative of a new family Caryocarididae Racheboeuf, Vannier et Ortega seems to be fully justified, particularly with regard to the configuration of the abdomen.

The homogeneity of the genus, however, may not be as perfect as stressed by Racheboeuf et al. (2000). Especially *Caryocaris? stewarti* Jell, 1980 is distinct from *Rhinopterocaris maccoyi* sensu Chapman 1903, and clearly shows unique, broadly leaf-like (or better fin-like) furcal rami (see Jell 1980, fig. 7) which are markedly different from those of other representatives of *Caryocaris* in which tail segments are known. A thorough revision of Ordovician phyllocarids, particularly those from Victoria would greatly contribute to the clarification of this question.

The carapace valves of *Caryocaris* show remarkable abilities to be deformed. Apart from longitudinal coiling of the whole carapace valves, local and cone-like coiling of entire valves or their fragments can be observed. The curvature of the anterodorsal horn of *Caryocaris zhejiangensis* Shen, 1986 may also result from the same type of deformation (a detailed study of better preserved material is needed).

The generic name *Caryocaris* is derived from the Greek *kari* = shrimp (gender feminine). Consequently, species names should have the corresponding endings, namely *Caryocaris oblonga* Gurley, 1896 or *Caryocaris delicata* Racheboeuf, Vannier et Ortega, 2000 as examples.

Occurrence: *Caryocaris* is a world-wide distributed genus (Vannier et al. in press) known particularly from the Lower and Middle Ordovician rocks of Europe (England, Scotland?, Bohemia, Norway, Germany), North America (Alaska, Nevada, Idaho, Canada), Asia (China – Zhejiang), Australia (Victoria, New Zealand) and South America (Bolivia, Argentina). It is reported to occur also in the Upper Ordovician of Peru (Bulman 1931). The last and rare occurrences of *Caryocaris* in the Barrandian are Upper Ordovician in age (unpublished new material). The youngest occurrence has been reported from the Lower Silurian of the Canadian Arctic (Cornwallis Island, Copeland 1967). Although the reference to *Caryocaris* is correct, the dating of the phyllocarid-bearing strata (Wenlockian according to graptolites found nearby) needs to be re-examined. The maximum development of *Caryocaris* clearly falls within the interval Arenigian–Llanvirnian (or better Arenigian to Darriwillian, as some frequent occurrences are younger than the original Llanvirnian).

Caryocaris subula Chlupáč, 1970

Plate I, figs. 1–4

1970 *Caryocaris (Rhinopterocaris) subula* sp. n., Chlupáč, p. 55–59, text-fig. 7, 8, 9 pl. 5, figs. 1–10, pl. 6, figs. 1–5, pl. 7, figs. 1–7.

2000 *Caryocaris subula* Chlupáč, 1970, Racheboeuf, Vannier et Ortega, p. 323, 331, text-fig. 13B.

Remarks: The description and affinities of this characteristic and frequent species have been already presented by Chlupáč (1970). The new material from the excavation at Praha – Červený vrch Hill is very similar to that from Praha–Jenerálka (Na Salátce, former brickyard quarry) where this species frequently occurs in roughly coeval level (lower part of the Šárka Formation, *Corymbograptus retroflexus* Zone).

Fifty relatively undistorted specimens were selected from a large amount of collected specimens. The length of their carapace (without anterior horn and posterodorsal spine) ranges between 3 and 10 mm, the dorsoventral width between 1.3 to 4.2 mm (the width seems to be more strongly affected by deformation than the length). The carapace horn is often entirely or partly broken off, but specimens with a well-preserved horn corresponding to the reconstruction (see Chlupáč 1970, text-fig. 7) are abundant in the new material described herein. Isolated anterior horns are commonly found as fragments along with broken anterior parts of isolated carapace valves.

Abdominal segments were not found in connection with the tail-pieces. Short segments are preserved as isolated bands, often fragmented. Abdominal segments connected with caudal spines are rare. Typical is the specimen on Plate I, fig. 4, which preserves 5 to 6 narrow segments of subquadrate outline (the two anteriormost fragmentary), followed by a conical telson (2.5 mm long) and a pair of furcal rami (4.1 mm in length; measured along the outer margin). The length of the conical telson of 8 other speci-

mens ranges between 1 and 4 mm, two specimens show a medial longitudinal keel but the effect of deformation cannot be excluded. Flame-like and flat furcal rami bear only seldom well-preserved, short, posteriorly directed spinules on the outer side; setae on the inner side of furcal rami were not observed (probably broken off during transportation?).

Although several hundreds of specimens were examined, none show the carapace valves in direct and clear connection with the abdomen. The situation is similar at all other Bohemian localities where *Caryocaris* occurs (see discussion below). Noteworthy is the above mentioned specimen, connected with caudal spines in close proximity with laterally flattened carapace valves (most probably the same specimen). This recalls two other specimens (ICH571, ICH599) previously described as *Caryocaris wrighti* by Chlupáč (1970, text-fig. 3) and confirms the conspecificity of the carapace valves with the abdominal parts repeatedly found close to them. The question of the number of abdominal segments extending outside from the carapace posteriorly, however, remains open (the abdominal part protruding from the carapace may not be necessarily as short as it is depicted in the reconstructions of *C. wrighti* and *C. subula* made by Racheboeuf et al. 2000, figs. 13A, B).

In agreement with other, previously described specimens of *C. subula*, our new specimens do not show typical longitudinal enrollment of *Caryocaris curvilata* and *C. wrighti* (see Churkin 1966, Chlupáč 1970). This is most likely due to the relatively smaller size (smaller than *C. wrighti*) and rather oval shape of the carapace valves of *C. subula* which were strengthened by the prominent anterior horn. However, the carapaces of *C. subula* and *C. wrighti* are both thin and evidently of the same composition. They are typically preserved as dark and glittering matter.

C. subula is by far the most frequent fossil find in the studied shales (Šárka Formation at Praha – Červený vrch Hill). Its remains are often concentrated on bedding planes or form clusters of several tens (often 20 to 50, sometimes more) of specimens. These peculiar occurrences are discussed in the paleoecology section of the present paper.

Caryocaris wrighti Salter, 1863

Plate I, figs. 5–8

Synonymy: see Chlupáč, 1970, p. 45.

Remarks: By comparison with *C. subula*, this typical and widely distributed species is markedly less common at the studied locality. The recently collected specimens agree in all main features with those previously described from the Bohemian Ordovician (Chlupáč 1970).

The characteristic features of *C. wrighti* are as follows: The pod-shaped carapace valves with simply pointed anterodorsal part without marked anterior horn, well-defined ventral border delimited by a border furrow, dorso-ventrally truncated posterior margin with two small (posterodorsal and posteroventral) spines and numerous (more than thirty) very tiny spinules tightly arranged be-

tween them. The abdomen consists of short segments of subcircular transversal cross-section and equal sagittal length (pretelson is not prolonged), a conical, posteriorly rapidly tapering telson, and flat, flame-like furcal rami with few (max. 5) short outer spines and numerous setae bordering the inner margin.

The largest carapace valves found in our new collections are compressed laterally (length = 23 or 24 mm, dorsoventral width = 9 mm). The length of other carapace valves ranges between 14 and 20 mm. These measurements fall within the common size ranges of *C. wrighti* given by Chlupáč (1970). Very obvious is the longitudinal enrollment of carapace valves which was well described in *C. curvilata* from Alaska by Churkin (1966) and also in *C. wrighti* from the Barrandian (Chlupáč 1970).

The collected caudal spines, namely telsons and furcal rami are similar to those described earlier (Chlupáč 1970). It is not certain that they belong to *C. wrighti*. These elements, when isolated, are difficult to distinguish from those of *C. subula*.

Palaeoecological and general notes

Caryocaris is a widely distributed crustacean in the Lower and Middle Ordovician. It is generally regarded a pelagic component of marine fauna, typically associated with graptolites in the graptolitic shale facies (Stormer 1937, Racheboeuf et al. 2000, Vannier et al. in press).

In the Ordovician of the Barrandian area, *Caryocaris* are confined to dark grey shales with silty intervals. *Caryocaris* often occurs in shales with strongly impoverished benthos. Typical examples were given by Chlupáč (1970) at Praha-Jenerálka (Na Salátce) and by our new exposures at Praha – Červený vrch Hill. At some localities it is associated with rather diverse benthic forms (trilobites, brachiopods, gastropods, hyolithids, bivalves and echinoderms). This is the case of classical localities near of Rokycany, such as Šárka (see Chlupáč 1970). This points to a certain tolerance or lesser dependence on depth conditions, which agrees with the wide geographic distribution of *Caryocaris*.

However, *Caryocaris* is almost invariably associated with the shale facies. *Caryocaris* is absent (or extremely rare) in the nearshore and high-energy, shallow-water sandstone (quartzite) facies of the Barrandian Ordovician (the Skalka Quartzite replacing the *Caryocaris*-bearing shale facies of the Dobrotivá Formation as a typical example).

Caryocaris has been generally regarded as a planktonic animal, although Bulman's (1964) opinion is more reserved. Chlupáč (1970) regarded *Caryocaris* as a probable epipelagic organism which may have been attached to floating algal thali in the upper photic zone near the water surface. This does not mean that *Caryocaris* was not an active swimmer (see Vannier et al. 1997), but its best life conditions were probably associated with algal carpets in the uppermost part of the water column. This explanation corresponds to the frequent occurrences of clusters of *Caryo-*

caris remains (e.g. our new locality). Recently, Racheboeuf et al. (2000) discussed the problem of exuviae and their tendency to coil longitudinally. Their conclusions are consistent with the mode of preservation of *Caryocaris wrighti* in the Barrandian.

The fact that no complete specimen with connected carapace and abdomen was found among hundreds of specimens collected or examined in the field indicates a post-mortem transportation. This is also supported by finds of large bedding planes crowded with *Caryocaris* remains, where complete carapace valves are present together with markedly fragmented remains (see Plate I, fig. 3).

The markedly impoverished and less frequent associated fauna consisting of graptolites, dendroids, small inarticulates and other rare fossils points to a pelagic environment episodically affected by currents whose direction cannot be reconstructed (e.g., from the linear arrangement of fossil remains or from the input of typical shallow-water inhabitants).

The grain-size gradients are low, and together with the fine lamination point to rather quiet conditions in deeper-water and dysoxic environments, not suitable for the benthos. These characteristics seem to correspond to the lower part of the Šárka Formation (study area) and cannot be generalized for the whole formation, for example the Bouček's (1927) interval 3 in the former Vokovice brickyard. Fauna from other classical fossiliferous localities of the Šárka Formation evidently reflects a more suitable environment with more diverse benthic assemblages (the Euorthisina Community sensu Havlíček 1982 = Euorthisina-Placoparia Community sensu Havlíček and Vaněk 1990, see also Havlíček 1998).

The extreme abundance of *Caryocaris* at the studied locality and elsewhere would fully justify the term "Caryocaris Shale". These shales differ from typical graptolitic shales in a lesser content of organic carbon (consequently, the colour is grey, not black), a higher amount of silt component, and less frequent graptolites whose frequency is far behind the remains of *Caryocaris*. According to the Boucot's (1975) classification the studied *Caryocaris*-bearing rocks in the studied section belong to the pelagic realm with Benthic Assemblage 6, most likely the open-shelf environment.

The wide and cosmopolitan distribution of *Caryocaris* has its counterpart in the Cambrian *Isoxys* Walcott, 1990 (see Williams et al. 1996, Vannier et al. 1997, Vannier and Chen 2000), whose morphology of carapace valves shows clear similarities (anterodorsal and posterodorsal spines, rather small size, etc.), though its systematic position was different and the Cambrian pelagic life generally less advanced.

Another remarkable feature concerns the stratigraphic occurrence of *Caryocaris*. The world-wide distribution of *Caryocaris* in the Arenigian and Darriwilian (former Llanvirnian to Llandeilian) strata (see Chlupáč 1970, Racheboeuf et al. 2000, Vannier et al. in press) contrasts markedly with the very sporadic occurrences of the genus in younger strata. A typical example is the Barrandian area,

where *Caryocaris* belongs to the most common fossils in the shale facies of the Klabava (Arenigian) up to Dobrotivá (“Llandeilian” = upper Darriwilian) formations. It becomes rare starting from the Libeň Formation correlated with the earliest Caradocian: it belongs to expressive rarities, although the lithology of the shale facies remains similar to that of the underlying formations (the same concerns younger units, namely the Vinice and Bohdalec formations). This might indicate an environmental change (possibly water chemistry or temperature), markedly unfavourable for *Caryocaris*. The decreasing frequency of *Caryocaris* may be related to some global event, which might have affected also other pelagic forms.

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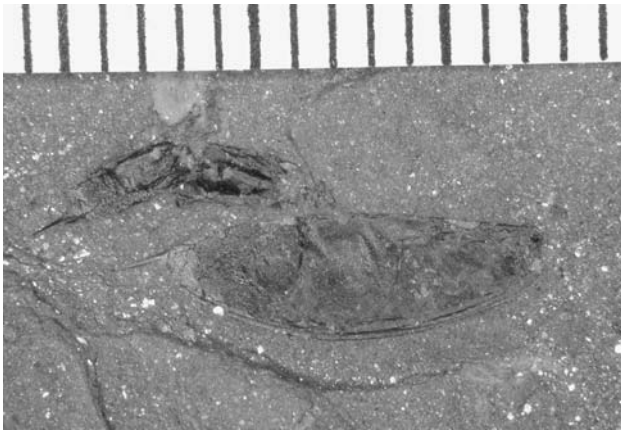
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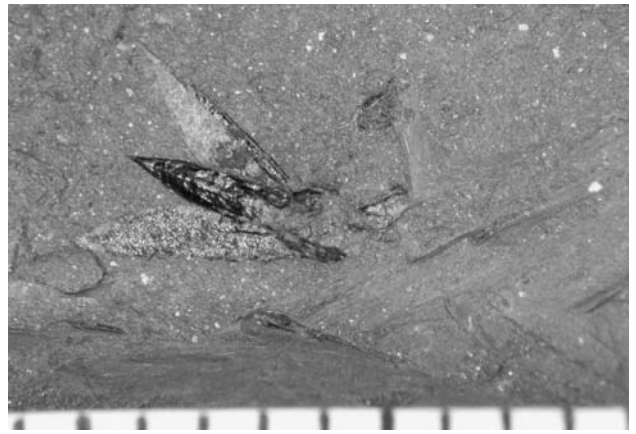
Plate I

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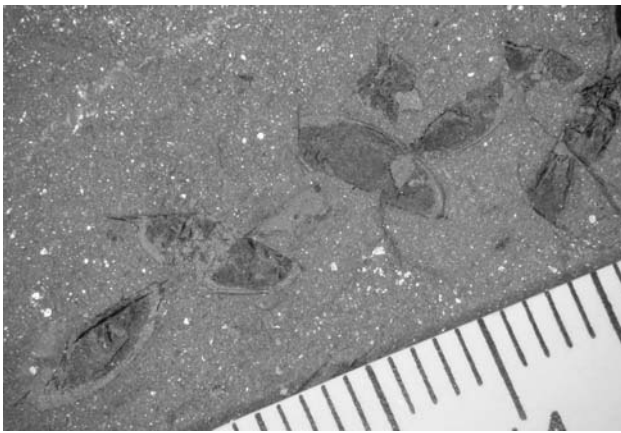
1 – *Caryocaris subula* Chlupáč (1970), left valve of carapace (Ich 7155) with deformed tailpiece and remains of posterior abdominal segments preserved in dark grey shale, Červený vrch Hill in Prague, Šárka Formation. 2 – *Caryocaris* cf. *subula* Chlupáč (1970), tailpiece and remains of posterior abdominal segments (Ich 7156) in dark grey shale, Červený vrch Hill in Prague, Šárka Formation. 3 – *Caryocaris subula* Chlupáč (1970), accumulation of carapaces (Ich 7157) in dark grey shale, Červený vrch Hill in Prague, Šárka Formation. 4 – *Caryocaris* cf. *subula* Chlupáč (1970), tailpiece and remains of posterior abdominal segments (Ich 7158) in dark grey shale, Červený vrch Hill in Prague, Šárka Formation. 5 – *Caryocaris* cf. *wrighti* Salter (1863), tailpiece and remains of posterior abdominal segments (Ich 7159) in dark grey shale, Červený vrch Hill in Prague, Šárka Formation. 6 – *Caryocaris* cf. *wrighti* Salter (1863), tailpiece and remains of posterior abdominal segments (Ich 7160) in dark grey shale, Červený vrch Hill in Prague, Šárka Formation. 7 – *Caryocaris wrighti* Salter (1863), left valve of carapace (Ich 7161) with tailpiece and remains of posterior abdominal segments in dark grey shale, Červený vrch Hill in Prague, Šárka Formation. 8 – *Caryocaris* cf. *wrighti* Salter (1863), tailpiece and remains of posterior abdominal segments (Ich 7162) in dark grey shale, Červený vrch Hill in Prague, Šárka Formation. Photographed by F. Vacek.



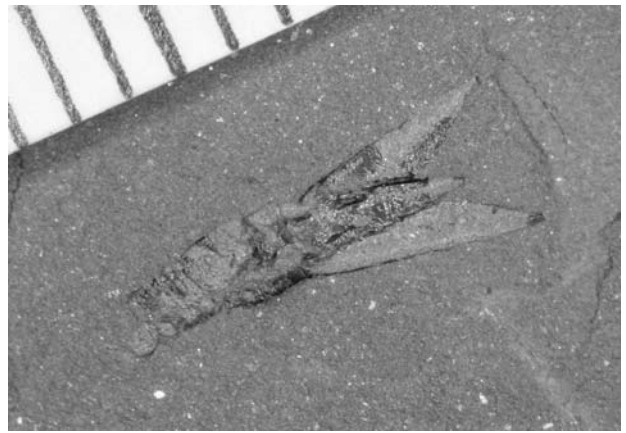
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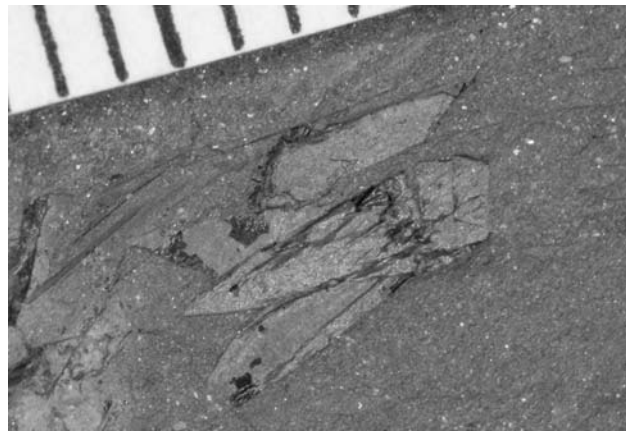
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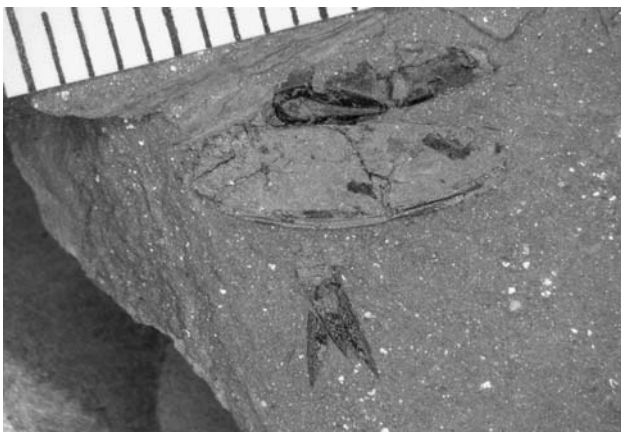
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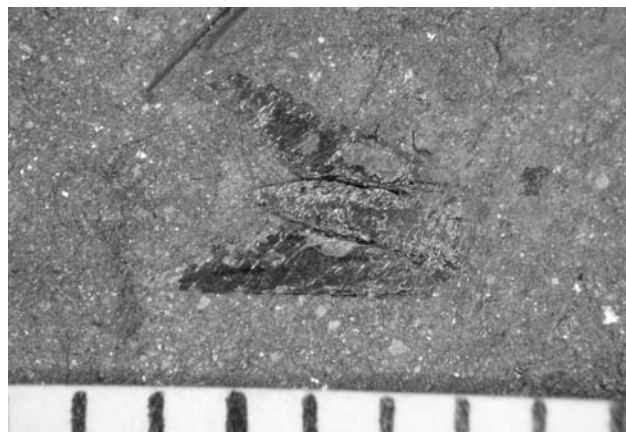
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