

MID DEVONIAN PHYLLOCARID CRUSTACEA FROM BOLIVIA

by PATRICK R. RACHEBOEUF

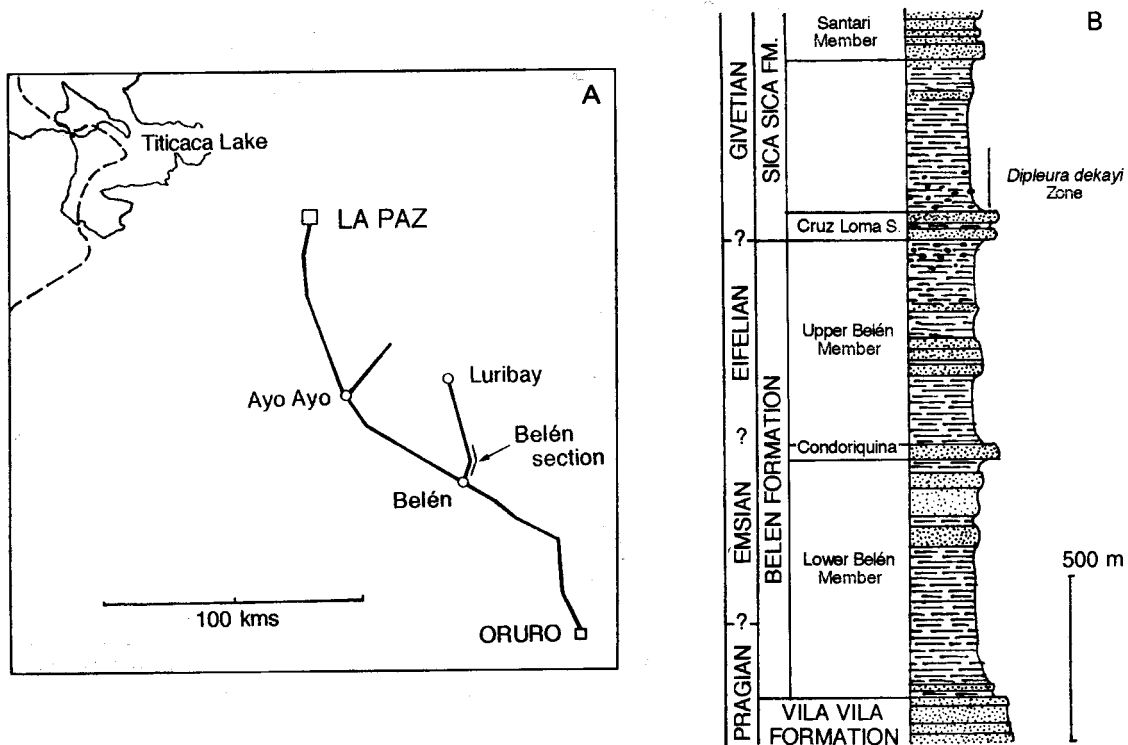
ABSTRACT. The Givetian *Dipleura dekayi* Zone of the Bolivian Altiplano, and adjacent stratigraphical levels, yield representatives of the phyllocarid genera *Echinocaris* and *Dithyrocaris*. The peculiar morphology and well-preserved original features of the exoskeleton allow erection of a new species, *Echinocaris spiniger* sp. nov. Discovery of a carapace with abdominal somites still connected allows identification of the corresponding tail piece and description of the complete exoskeleton of *Dithyrocaris oculus* sp. nov., probably one of the earliest representatives of the genus. Palaeobiological and taphonomic data regarding these species are discussed. Two other forms, represented by only few specimens from other isolated localities, are provisionally left in open nomenclature: *Echinocaris* sp. and *Dithyrocaris* sp.

NUMEROUS papers have been devoted to the description of phyllocarid taxa or to more general topics such as their evolution and palaeobiogeography. Despite this abundant literature, phyllocarid crustaceans remain poorly known and are probably much more diverse than previously established. Besides the general rarity of these fossils, our relatively poor knowledge is due partly to the fact that most taxa have been described only from isolated parts of the exoskeleton, mainly the tail piece, and little is known about their ontogeny. Species described from complete exoskeletons are few, and little data on intraspecific variability are available. As a consequence, the taxonomic value of many morphological characters is still uncertain. For such reasons any description of complete exoskeletons or of numerous isolated elements may prove to be significant for diversity, taxonomic, palaeoecological, evolutionary and palaeobiogeographical studies. This is the case for the Mid Devonian Bolivian phyllocarids described here.

Occurrence. Fossiliferous siliciclastic concretions occur at several lithostratigraphical levels within the Devonian sequence of Bolivia; these concretions are well known throughout the world for their well-preserved fossils. Many examples of trilobites, brachiopods, bivalves, conulariids and vertebrate remains are described in the literature. This is also true for rarer fossils, such as phyllocarids, which have only recently been described by Hannibal *et al.* (1994). These authors described and illustrated *Echinocaris* cf. *punctata* (Hall, 1863), *Dithyrocaris* cf. *insignis* Jones and Woodward, 1898, undetermined rhinocaridid abdomens and telsons, as well as mandibles. Due to their poor preservation or fragmentary condition, specimens were left in open nomenclature. Most of these materials were collected many years ago by L. Branisa and are now housed in various institutions: the United States National Museum (USNM), the American Museum of Natural History (AMNH), the Hunterian Museum of the University of Glasgow (GLAHM), and the Museum of Comparative Zoology, Harvard University.

In 1993 three concretions yielding phyllocarid remains were collected *in situ* in the Belén section, 25 m above the top of the Cruz Loma Sandstone, i.e. in the lower part of the Sica Sica Formation. These beds belong to the *Dipleura dekayi* Zone (Text-fig. 1b). The first concretion yielded a well-preserved right valve of *Dithyrocaris*, with three abdominal somites still connected. The second yielded the ventral external mould of an almost complete tail piece of the same genus. The third concretion yielded both articulated valves, although incomplete, of a specimen of *Echinocaris*.

Lengthy preparation using hydrochloric acid, needles, and an engraver-pen revealed that the right valve of *Dithyrocaris* exhibits several details that do not fit with the description of specimens



TEXT-FIG. 1. A, location map of the Belén section in the Bolivian Altiplano. B, corresponding lithostratigraphical column, with location of concretion levels and *Dipleura dekayi* Zone.

previously studied by Hannibal *et al.* (1994). Hence it was necessary to compare the newly discovered specimen with those which had been previously collected and described, after the latter had been prepared using the same method. It was clear that features and morphological details observed on the newly found carapace of *Dithyrocaris* were likewise evident on each of the other previously collected carapaces. All the material belongs to the same species and allows a complete description of the exoskeleton of *Dithyrocaris oculus* sp. nov., including the abdomen and tail piece; but no appendages, except for the mandible are known. In the same way, after preparation, the material of *Echinocaris* allows the description of a new species, *Echinocaris spiniger* sp. nov., co-occurring with *Dithyrocaris oculus* in at least one level.

Among the undetermined specimens illustrated by Hannibal *et al.* (1994, fig. 4.6) is a large tail piece of a rhinocaridid, probably of the genus *Dithyrocaris*, from the locality Achumani Alto (south of La Paz), the stratigraphical position of which remains uncertain. As indicated by the authors, this specimen (GLAHM A2793) is from a larger individual than those from the *Dipleura dekayi* Zone. It is re-illustrated for comparison, and described herein as *Dithyrocaris* sp. Another less complete specimen, similar in size and every aspect of its morphology (GLAHM 101283), comes from the locality Aiquile (Department Cochabamba), also of uncertain stratigraphical position. Both specimens undoubtedly belong to a rhinocaridid species distinct from *Dithyrocaris* from the *Dipleura dekayi* Zone and they are possibly from a different stratigraphical level. To ensure accuracy, only specimens which definitely or presumably come from the uppermost Belén Formation, and from the lower part of the Sica Sica Formation (Cruz Loma Sandstone and overlying siltstones, Givetian *Dipleura dekayi* Zone), are described herein.

Measurements and terminology follow those used by Rolfe (1962, 1969, 1981) and by Hannibal *et al.* (1994). New specimens are deposited in the YPFB collection, under numbers 'YPFB Pal',

Centro de Tecnología Petrolera, Santa Cruz de la Sierra, Bolivia. Other studied specimens are housed in the American Museum of Natural History (AMNH) and in the Hunterian Museum of the University of Glasgow (GLAHM = HMGU in Hannibal *et al.* 1994).

Stratigraphical background. Almost all known Devonian Bolivian phyllocarid occurrences are from the Belén and Sica Sica formations of the Altiplano region, assigned to the Emsian, although the upper part of the Sica Sica Formation may be Eifelian (Isaacson 1977). Such a stratigraphical assignment led Rolfe and Edwards (1979) to consider that representatives of the genus *Dithyrocaris* from the Sica Sica Formation had 'an earlier', unsuspected biostratigraphical occurrence... than previously known. More recently Isaacson and Sablock (1988) assigned an Eifelian age to the uppermost Belén Formation, whilst the whole of the Sica Sica Formation was considered to be Eifelian. Hannibal *et al.* (1994, pp. 62–63) concluded that Bolivian representatives of the genera *Echinocaris* and *Dithyrocaris* are among the earliest in the world.

The age of the Devonian sequence of Bolivia has been discussed recently, and a new vertical range proposed (Racheboeuf *et al.* 1993, 1994; Blicek *et al.* 1996). As a consequence of new palynological data and proposed lithostratigraphical correlations, an Eifelian age was assigned to the upper member of the Belén Formation and a Givetian age to the Sica Sica Formation, the Eifelian-Givetian boundary being placed provisionally just below or within the Cruz Loma Sandstone. Such results are in better agreement with the Givetian age of the *Dipleura* fauna in North America, and imply that representatives of both *Echinocaris* and *Dithyrocaris* are of about the same age as those in North America.

Most available Devonian phyllocarid specimens from Bolivia come from Branisa's zones of the Belén section of the Altiplano, about 120 km south of La Paz (Text-fig 1A): Belén 7-0, 7-7, 8-1, 8-3, C15. These zones are not easy to place precisely within the stratigraphical column, but according to Branisa (1965) and his personal communications to various authors, some of them can be clearly defined (see Babcock *et al.* 1987). The stratigraphical position of locality 7-0 remains uncertain and belongs to either the Belén or the Sica Sica Formation. 7-7 belongs to beds with *Taonurus candegalli* of the *Metacryphaeus venustus* Zone, lower part of the Cruz Loma Sandstone, lowermost beds of the Sica Sica Formation. Locality 8-3 corresponds to the Cierro Cieloloma section of the Belén section, and belongs to the Givetian *Dipleura dekayi* Zone of the Sica Sica Formation, above the Cruz Loma Sandstone. Locality 8-1 of the Belén section could not be precisely located; the only available information from Branisa is 'Middle Devonian'.

Among a collection of 37 concretions from these localities, the distribution of phyllocarid remains (mandibles excluded) is as follows: concretions with *Echinocaris* from localities 7-0 and 8-1 respectively yielded one and five specimens; those with *Dithyrocaris* from localities 7-7, 8-1, and C15, respectively yielded one, 15, 14 and one specimen. Although there is no stratigraphical order inferred from the increasing locality numbers, it appears clearly that the distribution of phyllocarid remains is not random: (1) phyllocarids are more abundant at localities 8-1 and 8-3; (2) representatives of *Dithyrocaris* are commoner than representatives of *Echinocaris*; (3) each genus is represented by a single species; (4) the distribution of phyllocarid remains per locality is strongly suggestive of a longer vertical range for *Dithyrocaris oculus* than for *Echinocaris spiniger*.

SYSTEMATIC PALAEOONTOLOGY

Suborder CERATIOCARINA Clarke, *in* Zittel, 1900

Family ECHINOCARIDIDAE Clarke, *in* Zittel, 1900

Genus ECHINOCARIS Whitfield, 1880

Type species. *Echinocaris sublevis* Whitfield, 1880, by original designation, from the Upper Devonian of Ohio.

Echinocaris spiniger sp. nov.

Plate 1, figures 1–10; Text-figure 2

1994 *Echinocaris* cf. *E. punctata* (Hall, 1863); Hannibal *et al.* p. 60, figs 2.1–2.6.*Holotype.* Tail piece and abdominal somites GLAHM A2790.*Derivation of name.* From the Latin 'spina' (spine) and 'gero' (to bear): an allusion to the strong lateral spinules on the telson.*Locality and horizon.* In the Belén section, just above the Cruz Loma Quartzite, in the *Dipleura dekayi* Zone (Branisa's zone 8-3), lowermost Sica Sica Formation, the same locality and level as most of the material studied by Hannibal *et al.* (1994).*Material.* The anterior part of the two valves of an articulated carapace (YPFB Pal 9290); both moulds of an almost complete tail piece with the two last abdominal somites displaced (GLAHM A2790); both moulds of an almost complete, articulated exoskeleton (AMNH 43516A–B), and an incomplete, crushed carapace (AMNH 43515A–B).*Diagnosis.* Echinocaridid without tubercles on the dorsal and posterodorsal lobes of the carapace. Telson with stout, spaced latero-dorsally inserted spinules, and two shallow longitudinal ventral furrows. Furcal rami with dorsal, ventral and inner furrows, the latter with a row of minute pits for insertion of setae.*Description*

Carapace. The carapace of the almost complete exoskeleton (AMNH 43516) is poorly preserved, except for its anterior region (Pl. 1, fig 5), and is about 35 mm long for an overall length of the exoskeleton about 85 mm. The only new available specimen (YPFB Pal 9290) exhibits about two-thirds of the left valve, and the corresponding dorsal region of the right valve, still articulated. The maximum preserved length is 40 mm and its estimated total length is about 50 mm. The external mould exhibits the anterior margin of the carapace which is very slightly convex forward, almost straight, truncated, and roughly perpendicular to the dorsal line. A narrow border is well developed. Antero-dorsally the border is a rounded rim which tapers progressively antero-ventrally, becoming narrower, and more flattened. The border is markedly geniculated inwards, at 90° from the plane of the valve, developing a flattened proximal wall, and bounded by a thin, narrow, ridge. The distal shelf could not be observed. The wall is very finely ornamented by very thin, almost imperceptible, longitudinal ridges. The surface of the valves is similar to that described by Hannibal *et al.* (1994), in the distribution and morphology of the lobes, as well as in their ornamentation, which is better developed in the posterior half of the valves, and composed of very small, low tubercles. However, the anterior slope of the anterodorsal lobe exhibits shallow, rounded, variably anastomosing canals which end in the furrow delineating the rounded border. The anterior half of the carapace is almost smooth and lobes are devoid of tubercles (Text-

EXPLANATION OF PLATE 1

Figs 1–10. *Echinocaris spiniger* sp. nov.; Givetian *Dipleura dekayi* Zone, Lower Sica Sica Formation, Belén section, Bolivian Altiplano. 1–4, YPFB Pal 9290; latex replica; incomplete articulated carapace. 1, general view; $\times 1.5$. 2, enlarged view of the postero-dorsal node; $\times 10$. 3–4, enlarged view of the anterior margin of the left valve, respectively exterior and interior; $\times 4$. 5–7, AMNH 43516; latex replica; almost complete, articulated exoskeleton. 5, general view of the dorsal side; $\times 1.5$. 6, dorsal side of the 5th to 7th abdominal somites and telson head; $\times 3$. 7, ventral side of 4th to 6th abdominal somites; note the ventral platform with two posterior spines and limb insertions on the 4th somite; $\times 3$. 8–10, GLAHM A2790; latex replica; well preserved tail piece, respectively in dorsal, dorso-lateral, and ventral views (with the 7th abdominal somite superimposed); note the large and spaced spinule bases on the telson, the shallow dorsal and ventral longitudinal furrows, and the articulatory dorsal and ventral condyles on the furcal rami; $\times 2$.

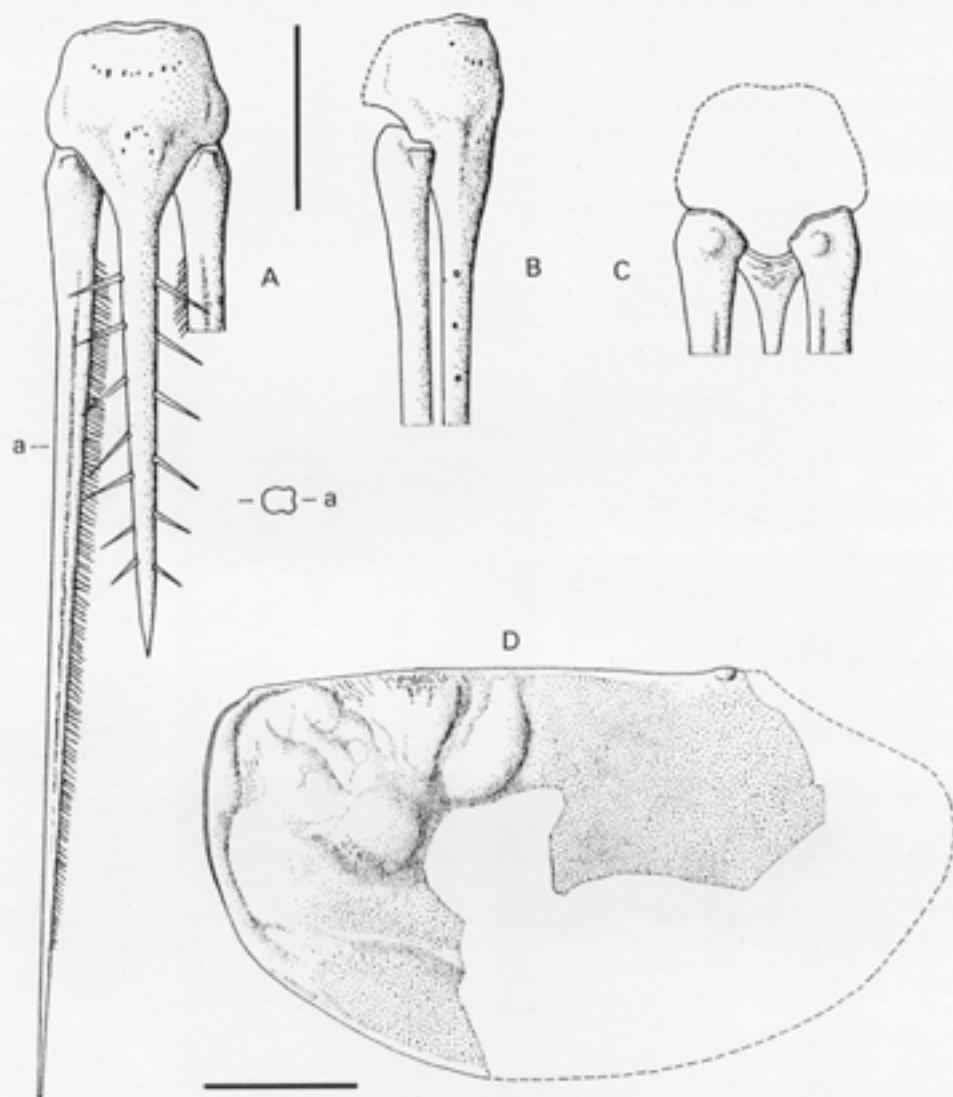
Fig. 11. *Echinocaris*, sp. from Branisa's zone 7-0, Belén section, GLAHM 101282; latex replica; abdominal somites 4 and 5 in ventral view; note the three spines on the ventral tubercle of the 4th somites; $\times 3$.



RACHEBOEUF, *Echinocaris*

fig. 2D; Pl. 1, figs 1, 5). The carapace is covered posteriorly by minute and dense granulations. Along the dorsal side of the left valve a small, rounded well-differentiated tubercle is developed. The ventral region of the carapace, as well as its posterior part, were not observed.

The corresponding internal mould of the left valve of specimen YPFB Pal 9290 is smooth, without any kind of ornament. The ridges, corresponding to the furrows separating the lobes on the external surface, are better developed. The most interesting feature is the development of two blade-like vertical expansions (Pl. 1, fig 4)



TEXT-FIG. 2. *Echinocaris spiniger* sp. nov.; Givetian *Dipleura dekayi* Zone, Lower Sica Sica Formation, Belén section, Bolivian Altiplano. A-C, reconstruction of the tail piece. *Camera lucida* drawings from specimen GLAHM A 2790. Broken lines refer to non-observed, hypothetical outlines. A, reconstruction of the tail piece in dorsal view; a, cross section of the left furcal ramus. B, anterior region of the tail piece in lateral view. C, anterior region of the tail piece in ventral view. D, tentative reconstruction of the outline of the left valve of the carapace. *Camera lucida* drawings from specimens YPFB Pal 9290, AMNH 43515, and AMNH 43516. Dotted line indicates the outline of the observed parts of the carapace. Broken line corresponds to a hypothetical outline of the carapace. Note the lack of tubercles on the lobes, the lack of granulation in the anterior region of the carapace, and the postero-dorsal node. Scale bars represent 10 mm.

in the antero-dorsal angle of the valves, close to the dorsal line and expanded from the rounded ridge corresponding to the external furrow separating the border from the valve surface. These lamellar processes are here interpreted as apodemes, insertion areas for muscles of the carapace.

Abdominal somites. The two moulds of the almost complete exoskeleton, AMNH 43516, were prepared carefully so that the ventral and dorsal sides of abdominal somites could be examined. The posterior edge of each somite is characterized by two strong postero-ventral lateral spines, and two main dorsal spines (Pl. 1, fig. 6). The latter are 2.6–2.9 mm apart and two smaller spines are inserted between them on each side of the plane of symmetry. On their ventral side, somites 6 and 7 exhibit a well differentiated, transversely elongated, convex anterior tubercle. Abdominal somites are finely ornamented dorsally with numerous small granulations, and they are almost smooth ventrally. The 4th abdominal somite is 3.6 mm long and 9.36 mm wide. Its ventral side exhibits a relatively small, prominent ventral tubercle with two postero-lateral spines and no antero-medial spine. Limb insertions are markedly oval, and obliquely displayed. Their maximum width is 3.27 mm, almost perpendicular to the longitudinal axis, while their length is 2.02 mm. Somites 5, 6 and 7 are, respectively, 4.2 mm, 5.6 mm and 9.5 mm long. Somites 6 and 7 are, respectively, 6.24 mm and 4.48 mm wide.

Telson and furcal rami. The head of the telson of specimen AMNH 43516 is 6.24 mm wide. The telson of specimen GLAHM A 2790 is 32 mm long. At its anterior margin, the head is 6 mm wide. It widens posteriorly up to 9 mm before it narrows to 2 mm, at the site of insertion of the furcal rami. Telson head convex, globose, with two lateral and two posterolateral shallow furrows. Dorsal side of the telson with two rows of small circular or elongated depressions. The anterior row is weakly arched, convex posteriorly, while the posterior row is strongly arched, posteriorly concave, horseshoe-shaped (Text-fig. 2A). Telson axis sub-cylindrical in cross section, with straight lateral margins and two shallow longitudinal ventral furrows, getting progressively narrower up to its spinose posterior extremity. Stout spinules are inserted latero-dorsally on each side of the telson. Spinules are widely spaced and they are not inserted in a longitudinal furrow. They number seven on the left side of the telson with intermediate spaces varying from 2.5 mm to 1.8 mm; spacing decreases backwards. Spines are not symmetrically inserted, but alternate either side of the telson, except for the last posterior two spinules which are almost opposed. Ventral platform not observed. The ventral side of the telson is weakly convex in cross section and smooth.

The maximum preserved length of the furcal rami is 28 mm. Their head is sub-cylindrical to oval in cross section and 3 mm wide, with well differentiated dorsal and ventral articulatory condyles (Text-fig. 2B–C). Lateral margins of furcal rami are straight and narrow posteriorly. At 5 mm posterior from their anterior extremity they are 2 mm wide, and at 23 mm, 1 mm wide. Furcal rami are rod-like, sub-circular in cross section, with three shallow longitudinal furrows producing a clover-leaf-like cross section. The outer lateral margin is rounded and larger than the other two lobes defined by the longitudinal furrows. The inner furrow, which faces the telson, bears small pits which are spinule or setal insertions. They number 5 per mm and their diameter is about one-quarter the diameter of the pits observed on the telson. If we consider that the furcal rami are regular in shape and that their width regularly decreases up to their extremity, their total length could reach 50 mm, i.e. about one-and-one-half times the corresponding telson length.

Remarks. The generic assignment of the carapace was established by Hannibal *et al.* (1994), and there is no doubt about the conspecificity of the newly described specimen which comes from the same level and locality, the *Dipleura dekayi* Zone of the Belén section. Hannibal *et al.* (1994) tentatively assigned his material to *E. punctata* (Hall, 1863), based on a strong overall resemblance in shape, ornamentation and relative proportions of carapace lobes and abdominal somites. However, the authors noted differences in the morphology of the dorsal and posterodorsal lobes of the carapace, as well as on the third last abdominal segment. The development of strong, latero-dorsal spines on the telson is undoubtedly one of the most original features of the Bolivian form. Such a peculiar feature is very different from that illustrated by Hall (1863, pl. 1, fig. 2) in '*Ceratiocaris armatus*' and has not been described in other representatives of *Echinocaris*. This character, added to the differences emphasized by Hannibal *et al.* (1994, p. 62), makes the Bolivian form a new species, distinct from *E. punctata*.

Echinocaris sp.

Plate 1, figure 11

Material. The external mould of the ventral side of three incomplete abdominal somites (GLAHM 101282), locality 7-0 of Branisa, Belén section; unknown stratigraphical position.

Comparison. This specimen is left in open nomenclature due to its fragmentary nature. Moreover, the ventral tubercle of the (?)4th abdominal somite exhibits three stout posteriorly directed spines, one antero-medial and two postero-lateral. This character distinguishes this form from *Echinocaris spiniger* which lacks the antero-medial spine on the ventral tubercle of 4th somite. However, the taxonomic significance of this character remains poorly known, and it could be related to dimorphism.

Suborder RHINOCARINA Clarke, *in* Zittel, 1900

Family RHINOCARIDIDAE Hall and Clarke, 1888

Genus DITHYROCARIUS Scouler, *in* Portlock, 1843

Type species. *Argas testudineus* Scouler, 1835, from the Lower Carboniferous of Scotland.

Dithyrocaris oculus sp. nov.

Plates 2-3; Text-figures 3-5

1994 *Dithyrocaris* cf. *D. insignis* Jones and Woodward, 1898; Hannibal *et al.*, p. 63, figs 4.1, 4.3-4.4.

Holotype. Both external and internal moulds of the left valve of a probably complete, articulated carapace, AMNH 44692.

Locality and Horizon. Lower part of the Sica Sica Formation within the lowest 30 m above the Cruz Loma Sandstone, in the Belén section of the Bolivian Altiplano, c. 120 km south-east of La Paz; Givetian *Dipleura dekayi* Zone.

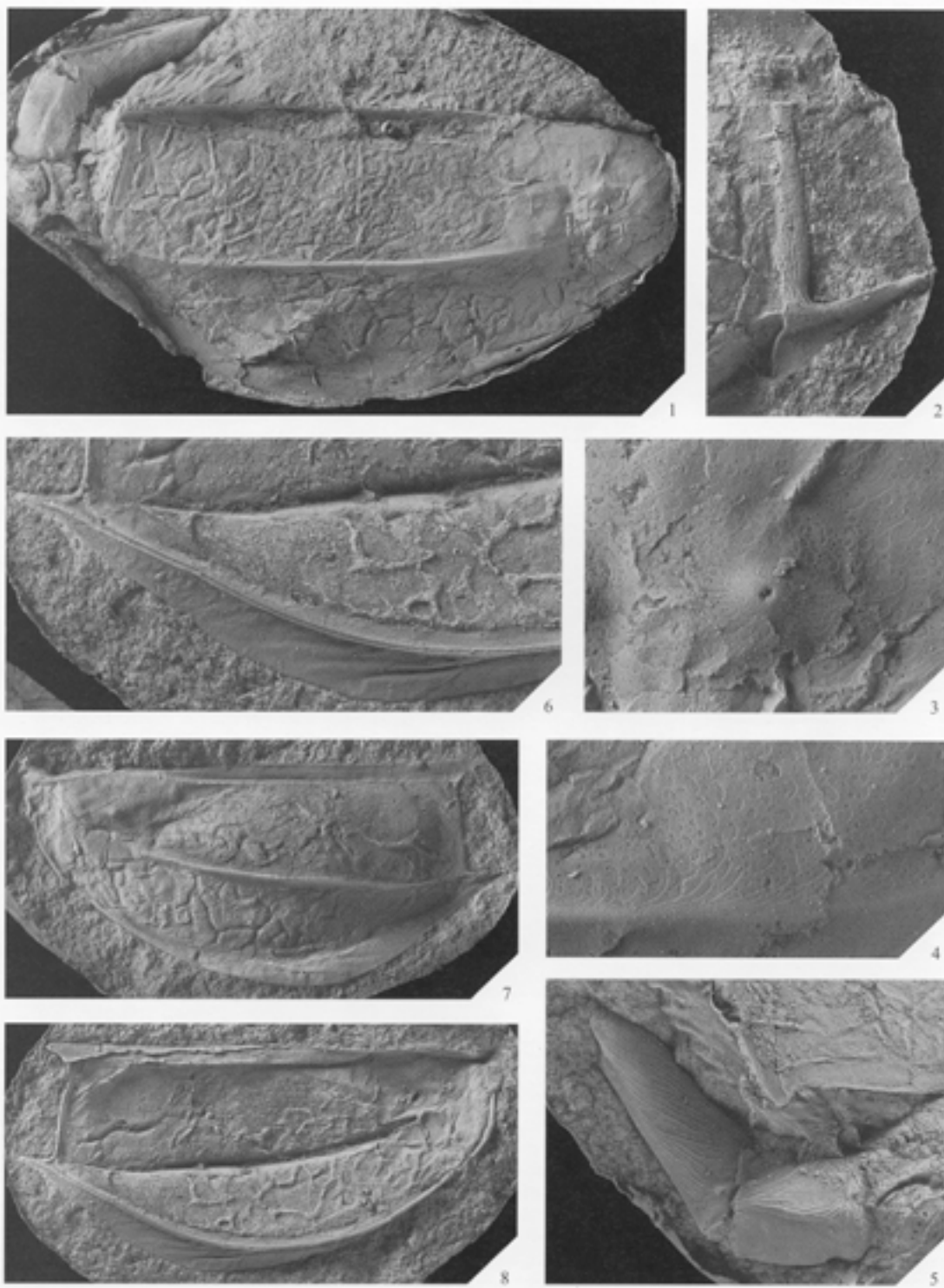
Derivation of name. From the Latin *oculus*, 'which has eyes'; alluding to the presence of the ocular tubercle.

Material. A total of 35 concretions has been studied; 12 of them yielded more or less complete isolated or articulated valves; eight abdominal segments, alone or in connection with the carapace or with the tail piece; 11 tail pieces, and nine mandibles, whilst five other concretions yielded valve fragments only.

Diagnosis. *Dithyrocaris* with a single, very weakly curved, mesolateral carina and well-developed posteroventral spine. Ventral margin regularly rounded, with a wide, smooth, and flat border. Ocular tubercle well differentiated. Median dorsal plate almost smooth, with well differentiated posterodorsal node. Doublure shelf very narrow. Carapace ornamentation very discrete, mainly made of curved, obliquely, postero-ventrally oriented lines, without any granulation. Abdominal somites with very thin ornamentation of anastomosed, anterodorsally-posteroventrally directed oblique lines. Limb site on 5th somite. 6th somite with lateroventral carina and ventral

EXPLANATION OF PLATE 2

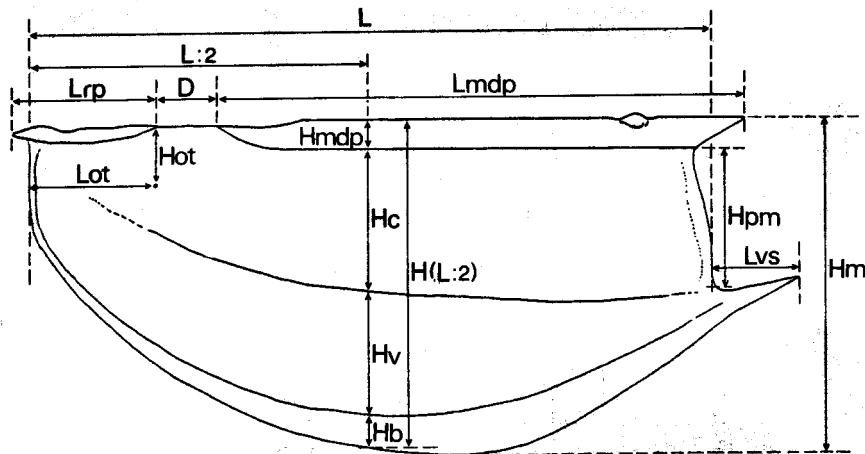
Figs 1-8. *Dithyrocaris oculus* sp. nov.; Givetian *Dipleura dekayi* Zone, Lower Sica Sica Formation, Belén section, Bolivian Altiplano. 1, 3-5, YPFN Pal 8432; latex replica; right valve of a large specimen with abdominal somites 5-7 still connected. 1, general view; $\times 2$. 3, enlarged view of the 'ocular' tubercle; $\times 10$. 4, enlarged view of the anterior part of the mesolateral carina showing the ornament and the smooth nature of the carina; $\times 10$. 5, enlarged lateral view of abdominal somites 6 and 7; $\times 3$. 2, AMNH 44693; latex replica; detail of the posterior margin of a left valve; $\times 3$. 6-8, AMNH 44692; latex replica; left valve. 6, detail of the postero-ventral doublure; $\times 4$. 7, external mould; note the location of the postero-dorsal node; $\times 2$. 8, internal mould; $\times 2$.



RACHEBOEUF, *Dithyrocaris*

TABLE 1. *Dithyrocaris oculus* sp. nov.; Givetian *Dipleura dekayi* Zone, Lower Sica Sica Formation, Belén section, Bolivian Altiplano. Outline of the left valve of the carapace showing the position and orientation of measurements (above), in millimetres. Asterisks in table refer to estimated measurements.

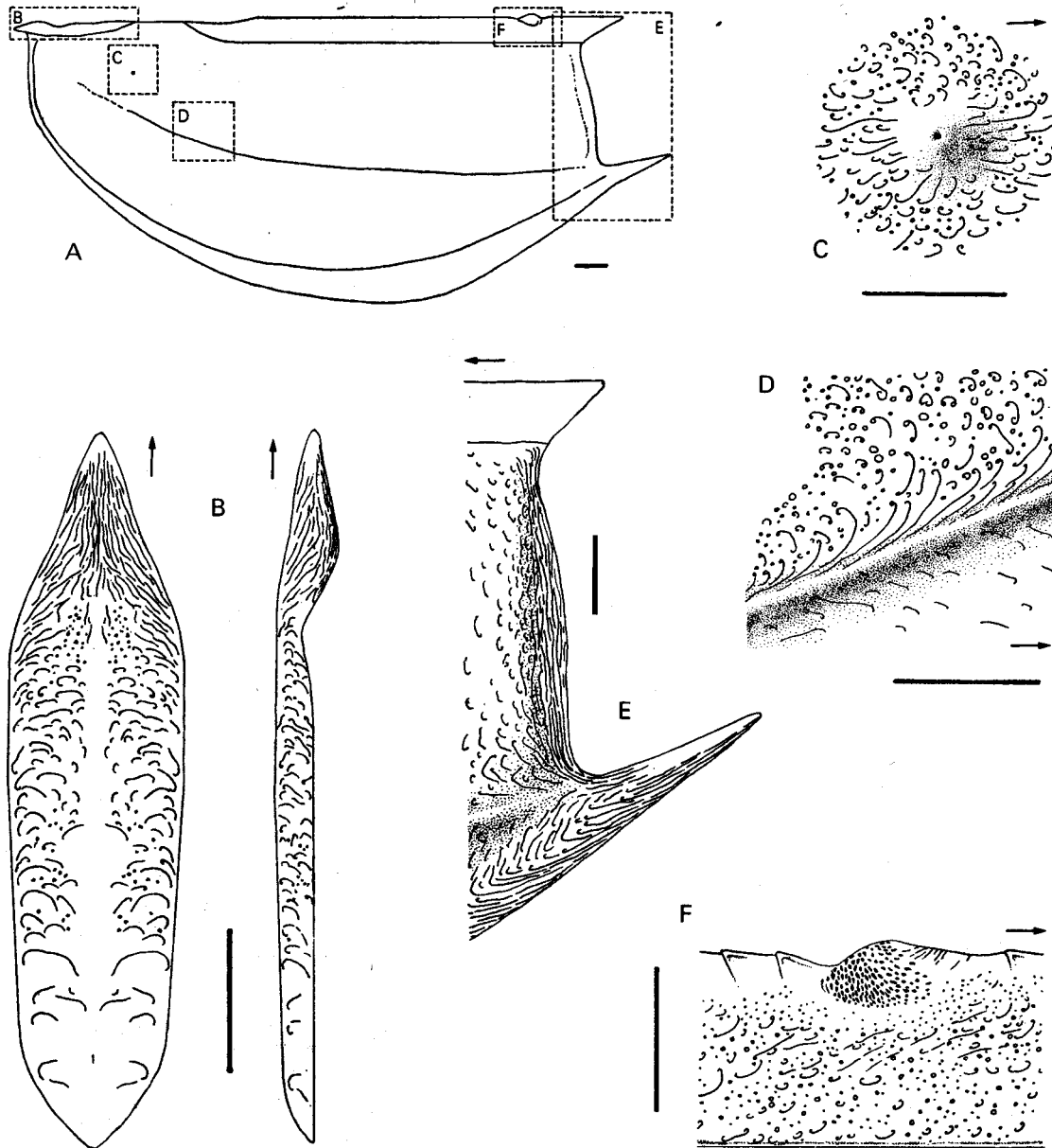
	YPFB 8432	AMNH 44692	AMNH 44693	AMNH 44694	GLAHM A2791	GLAHM 101261	GLAHM 101263	GLAHM 101272	GLAHM 101278
L	47*	37	38	—	43*	35	27*	35*	27.5
Hm	25	18.5	20.8	21	23*	16*	13	18	13*
H(L:2)	23.4	19.9	20.5	21*	—	—	13.1	—	—
Hmdp	2.3	1.8	2.1	1.6*	1.9	1.8	1.3	1.6	—
Hc	10	9.5	8.8	9.3	9.6	—	5.2	7.0	—
Hv	8.5	6.6	7.5	8.0	8.7	—	4.7	6.0	—
Hb	2.8	2.0	2.1	2.1	—	—	1.9	—	6.0
Lmdp	35	27	—	—	33.5	—	21.3	29.3	—
Lrp	—	8.0	—	—	—	—	—	8.5	5
Wrp	2.2	1.7	—	—	—	—	—	1.7	—
D	4?	3.0	—	—	—	—	2.3	2.6	2.2
Lvs	—	3.6	5.2	4.1	—	3.5	3.2	—	—
Hpm	9.2	8.0	8.2	9.0	9.1	7.0	5.8	7.5	—
Lot	7*	6.5	7.5	—	—	—	—	—	—
Hot	5.4	3.8	4.0	—	—	—	—	3.6	—



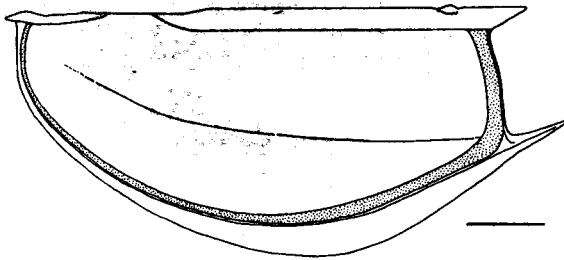
ornamentation. 7th somite sub-cylindrical, smooth ventrally. Telson long and narrow with acute extremity, two dorso-lateral shallow longitudinal furrows, and two rows of small spinules. Furcal rami typical for the genus, one-and-one-half times longer than the telson.

Description

Carapace. The smallest observed carapace is 27 mm long and c. 13 mm (estimated) high, whilst the largest is c. 50 mm long, including posteroventral spine, for a corresponding height of c. 25 mm, measured from midline to ventral border, including the lateral side of the median dorsal plate. Approximate length/height ratio of 2.0, varying between 1.8 and 2.1. Maximum height of the valve located at about three-fifths the valve length from the anterior border. Anterior margin regularly convex, bounded by a narrow rounded border, becoming sub-perpendicular to midline dorsally. Ventral margin weakly, regularly convex, with well differentiated, flattened, ventral border widening posteriorly, up to 4 mm high, posteriorly merging into a large, triangular, flattened, up to 4.5 mm long posteroventral spine. Dorsal margin of the spine in the prolongation of the mesolateral



TEXT-FIG. 3. *Dithyrocaris oculus* sp. nov.; Givetian *Dipleura dekayi* Zone, Lower Sica Sica Formation, Belén section, Bolivian Altiplano. A, schematic reconstruction of the carapace. Rectangles with letters indicate the location of enlarged details B to F. B-F, *Camera lucida* drawings showing details of the morphology and ornamentation; arrows indicate the front of the carapace. B, AMNH 44692, rostral plate in dorsal and lateral views (the ornamentation could not be observed along the longitudinal axis, left blank). C, YPFB Pal 8432, 'ocular tubercle' of right valve. D, YPFB Pal 8432, ornamentation of the right mesolateral carina. E, AMNH 44693, posterior part of left valve. F, GLAHM 101272, posterior part of the right side of median dorsal plate, showing curved ornament, posterodorsal projections of the dorsal carina, and the posterior node. Scale bars represent 2 mm.



TEXT-FIG. 4. *Dithyrocaris oculus* sp. nov.; Givetian *Dipleura dekayi* Zone, Lower Sica Sica Formation, Belén section, Bolivian Altiplano. Reconstruction of the inner side of right valve of carapace, showing the doublure. Doublure shelf stippled, separated from the doublure wall by the corrugated groove. Scale bar represents 5 mm.

carina. Posterior margin of the valve at about 100° with midline, with a fairly well developed rounded border, up to 2 mm wide, very weakly concave dorsally, then weakly sinuous or almost straight towards posteroventral spine. Measurements are given in Table 1.

The rostral plate was observed on four specimens. It is completely preserved on specimens AMNH 44692 and GLAHM 101272, whilst only its posterior half is preserved on specimens GLAHM 101262 and YPFB Pal 8432. The plate is weakly arched in cross section in its posterior part which is about two-thirds its total length. The anterior part of the plate is elevated, markedly triangular in cross section, ending anteriorly in a stout head, just extending beyond the anterior margin of the valve (Text-fig. 3B). Interval of 2.6 mm between the rostral plate and the median dorsal plate. Median dorsal plate well developed, long and relatively narrow, weakly arched in its anterior 3 mm, then becoming triangular, roof-shaped, in cross section with a well differentiated median dorsal carina, and posterior pointed termination. The maximum height of the plate is 2.3 mm. The dorsal longitudinal carina is crossed by oblique, weakly developed, chevron-like lines, the strongest of which develop short spine-like, posteriorly directed, expansions of the carapace (Text-fig. 3F). These very small projections number 3 to 4 per mm. At a distance between 4.1 mm and 5.8 mm from its posterior spinose extremity, the median dorsal plate exhibits a small node developed on both sides of the carina (Text-fig. 3F). This structure, described below, could not be observed on the internal moulds. Only one well differentiated, weakly curved, narrow, rounded, mesolateral carina inclined at about $5-10^\circ$ to the dorsal margin, originating anteriorly below the 'ocular' tubercle, or just anterior of it, and terminating posteriorly in the prolongation of the posteroventral spine. Length of the carina about 39 mm. At three-fifths the valve length from anterior margin, the carina is located at 53 per cent. the total valve height from dorsal midline.

A relatively small, slight, yet well differentiated, and perforated 'ocular' tubercle could be observed on six valves. It is located 6.5–7 mm from the anterior margin of the valve, usually straight below the posterior extremity of the rostral plate, or slightly behind this point, and at a distance between 3.6 mm and 5.4 mm from the midline, i.e. at about one-third the valve height measured (Text-fig. 3A). The hole in the centre of the tubercle is also present on the internal mould, indicating a perforation through the exoskeleton (Text-fig. 3C). However, the 'ocular' nature of the tubercle remains unclear, and even unlikely if we refer to the body plan of most crustaceans in which eyes always occupy an anterior location.

Five internal moulds display the doublure of the carapace. The doublure is well differentiated but relatively narrow, and elaborated into a proximal wall and a distal shelf separated by a narrow corrugated groove (Text-fig. 4). The doublure wall is similar to the external ventral border in size and morphology. The doublure shelf is relatively narrow, not exceeding 1.5 mm wide, i.e. *c.* one-third the maximum width of the wall. The width of the doublure shelf is constant and regular ventrally and posteriorly; it gets narrower anteroventrally and anteriorly, to 0.4 mm. Both wall and shelf are flat, smooth, devoid of any ornamentation. The groove is very narrow, *c.* 0.25 mm wide, mainly developed in the ventral part of the carapace, and bounded by two well differentiated ridges. The ventral ridge terminates at the extremity of the posteroventral spine, while the dorsal ridge curves dorsally to connect the posterior edge of the valve. The corrugated groove is not developed in the anterior part of the valve where the doublure is narrow and rounded.

Abdominal somites. Six concretions yielded abdominal segments, isolated or still connected with either the carapace or the tail. They correspond to somites 5, 6 and 7. Fragments of somite 4 have been observed but they are so poorly preserved that they cannot be used for description or reconstruction. Two specimens of somite 5 have lengths of 3 mm (GLAHM 101250) and 3.1 mm (GLAHM 101255). Ornamentation of somite 5 exhibits typical sinuous lines perpendicular to the longitudinal axis dorsally, bending backwards postero-ventrally. Ventral side of the somite almost smooth, with a markedly convex ventro-central tubercle, with sub-elliptical limb insertions similar to those described by Rolfe (1981). Centrovventral tubercle surrounded by a narrow furrow. Median part of ventral side not preserved (GLAHM 101255, Text-fig. 5r; Pl. 3, figs 2–3). Somite 6 is

4.5–8 mm long and 6 mm high, sub-cylindrical and shows a well differentiated, narrow, weakly pronounced, and sigmoid ventrolateral carina. This ridge originates anteriorly, posterior to the anterior lateral socket. Ornamentation dorsally chevron-like along the longitudinal axis. On the anterior part of the somite, lines are almost perpendicular to the somite axis whilst they become progressively oblique postero-ventrally. In the anterior part of the somite, sinuous dorso-lateral lines are deflected strongly backwards near the carina, which they do not cross. Ventrally, the ornamentation comprises thin, weakly pronounced lines, chevron-like anteriorly. The curvature along the midline become progressively reversed backwards whilst the ornamentation disappears progressively posteriorly, along the longitudinal axis (Text-fig. 5G–H). Somite 7 is 4.8–18 mm long, with a corresponding mean height of 2.4–6.8 mm (see Table 2). Somite 7 is anteriorly almost cylindrical in cross section, becoming sub-triangular, rounded posteriorly, devoid of lateral carina. The anterior lateral socket is relatively small, circular and smooth. Ventrally, the posterior part of the somite is depressed where it articulates with the head of the telson. The two antero-ventral condyles are prominent and rounded. Ornamentation of somite 7 is chevron-like dorsally, and postero-ventrally oblique on the flanks, whilst the ventral side is smooth, devoid of any sinuous lines (Text-fig. 5E–F). The length ratio between somite 7 and somite 6 of the same specimens lies between 0.56 and 0.59 (three measurements), while between somite 6 and somite 5 it is 0.6 (two measurements).

Tail piece. Eleven variably preserved specimens were available for description. The telson head is relatively wide, rounded, sub-semicircular in cross section, with weakly convex lateral margins. The telson becomes progressively narrower posteriorly; while the lateral margins become concave and the section becomes triangular. A longitudinal median carina, then two longitudinal lateral, shallow, rounded, furrows, differentiate progressively from the head, and extend posteriorly up to its acute extremity. Lateral margins are straight, very low-angled (about 5° to each other), and bear a very narrow groove in which very small spinules are inserted (Text-fig. 5B). A complete small telson (GLAHM 101250) is 14.5 mm long for a head which is 3 mm wide. Lateral spinules number 6 per mm. Spinules preserved on specimen GLAHM 101271 are 0.2–0.3 mm long. Ventral side of telson concave in its posterior part with a shallow median longitudinal groove, becoming flat to weakly convex posteriorly. Ventral platform sub-triangular, longitudinally depressed, with straight lateral margins and a rounded posterior free margin. Anterior part of the ventral platform with a relatively wide, V-shaped groove (Text-fig. 5C). Head of the telson ornamented by oblique, chevron-like lines which curve dorsally in the plane of symmetry (Text-fig. 5B).

Furcal rami very long and narrow, but only specimen YPFB Pal 8433 shows an almost completely preserved furca. The head of the telson is broken, and its total length is more than 21.5 mm. Furcal rami are *c.* 30 mm long (estimated). In specimen GLAHM 101250 furcal rami head is 1.5 mm wide and its reconstruction suggests that furcal rami are at least one-and-one-half times longer than the telson, i.e. *c.* 21.75 mm for a telson length of 14.5 mm. The length: width ratio of the telson is *c.* 4.5; that of the furcal rami is *c.* 14.5. Furcal rami flattened in cross section, with a rounded outer lateral edge. Dorsal side of the furcal rami with a deep, narrow, smooth, longitudinal groove, very close and parallel to the inner margin (Text-fig. 5B). Inner margin with a very narrow and deep groove in which spinules are inserted, as one the lateral margins of the telson. Anterior part of furcal rami ornamented by oblique lines on both ventral and dorsal sides. Specimen YPFB Pal 8433, found in the *Dipleura dekeyi* Zone of the Belén section, lacks the ornamentation on the anterior ventral region of the furca, and furca are slightly bent outwards in their distal region. These two characters may possibly be related to sexual dimorphism rather than indicating a distinct species. Comparable differences related to sexual dimorphism are known in the recent leptostracan *Nebalia bipes*. Males have longer setae and paddles than females (Vannier *et al.* 1997).

Mandibles. Concretion GLAHM 101255 yields three abdominal segments, the tail piece and the two mandibles, undoubtedly belonging to *Dithyrocaris*. Palp foramen relatively large with respect to the size of the grinding surface, and anteriorly placed. Grinding surface not easy to observe because acicular minerals are often developed on tubercles. Gnathal lobe regularly arcuate, with five well differentiated denticles and (?) one large, posterior, molar denticle. Incisor process high, well developed, followed by one simple, less elevated, conical denticle. Third and fourth denticles with two cusps. Molar denticle transversely ridged.

Ornamentation. The ornamentation of *Dithyrocaris oculeus* sp. nov. is very discrete, delicate, and varies from one part of the exoskeleton to another. It differs strongly between carapace and abdomen. Details are given in Text-figures 3 and 5. Two main types of microsculptures have been recognized on the carapace. The first type, located in the anterodorsal part of the carapace, above the mesolateral carina, and around the 'ocular' tubercle, is made of very small circular or sub-circular ridges, which open progressively towards the mesolateral

carina, producing volutes (curled ridges), which increase progressively in length (Text-fig. 3C–D). These volutes are always variably oblique to the dorsal margin. They have initially a dorso-anterior direction, then they turn progressively dorso-posteriorly, their ventral extremity progressively becomes unrolled, and they tend to become parallel to the carina which they never cross (Text-fig. 3D). These curved ridges occur radially on the flanks of the ‘ocular’ tubercle. Small, rounded, similar microsculptures appear again just below the mesolateral carina, which is always smooth. They increase in length progressively while their ventral extremity uncoils, and extend to the ventral border.

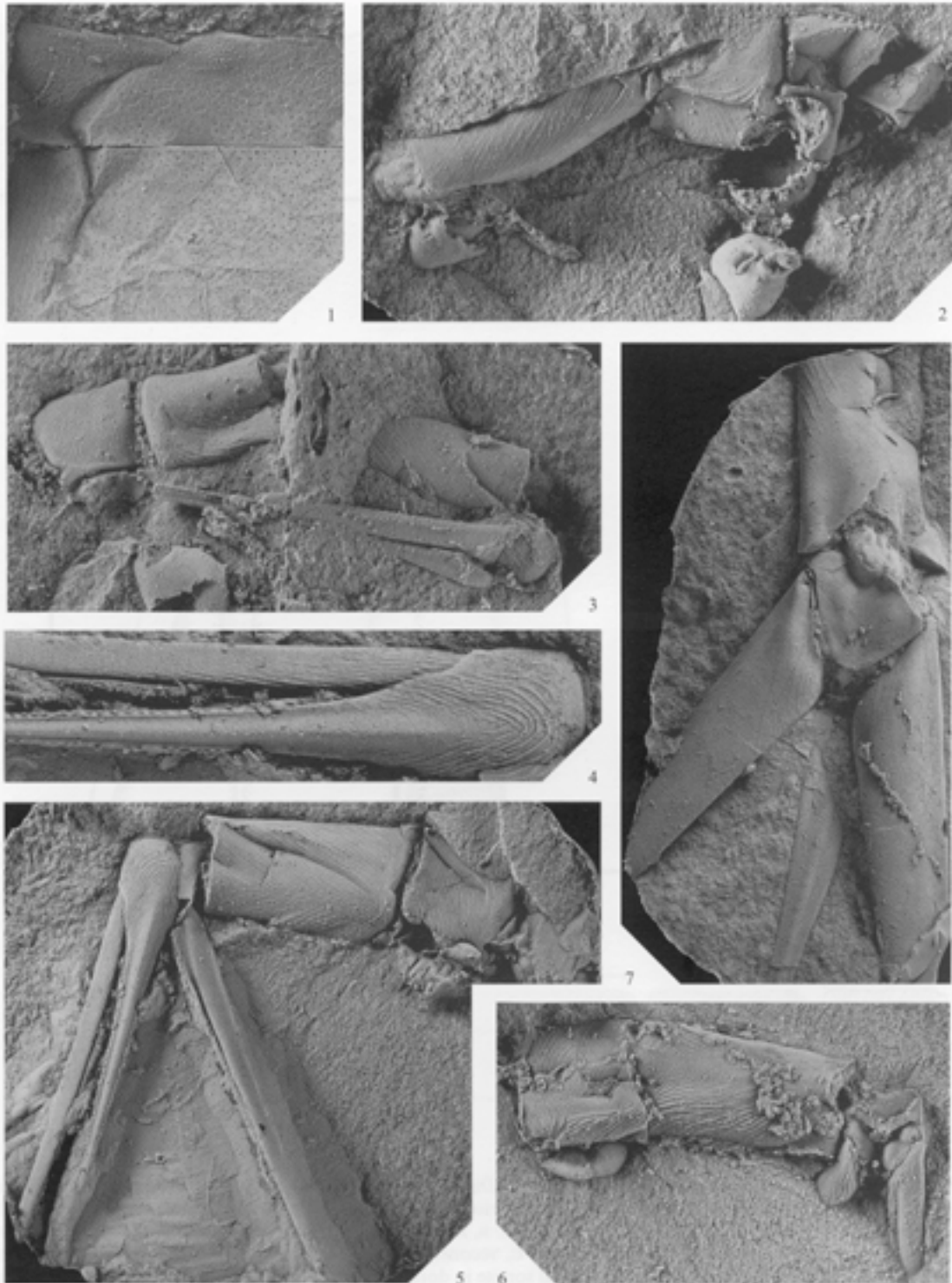
The second type of ornamentation is developed mainly on the anterior and anteroventral rounded rims as well as on the posterior margin. In the anterior part of the carapace, it is composed of sinuous, terrace-line-like ridges, initially parallel to the anterior margin of the carapace, then progressively curving backwards ventrally, and orientated at *c.* 45° to dorsal margin, crossing the anteroventral rounded rim, then extending with the same orientation on the ventral flat border, where the ridges are less prominent. The same kind of ornamentation is developed on the posteroventral spine as well as on the posterior margin to which they are more or less parallel (Text-fig. 3E).

The abdominal region (pleomeres 5–7) exhibits a different, typical, better developed ornamented pattern, which is common to many phyllocarid Archaeostraca and comparable to the ornamentation of many burrowing organisms. This ornament consists of a pattern of linear, sinuous, terrace-line-like ridges, roughly parallel to each other, and at 45° to the axis of each abdominal segment. These ridges are variable in length; some increase by intercalation (Text-fig. 5). They are not as developed as in *Dithyrocaris quinii* Copeland, 1967 where they form true cuestas, interpreted herein as possible features to prevent the animal from back slippage during the burrowing phase (Vannier *et al.* 1997). In the new species, the function of these structures was probably similar, although no other evidence for burrowing habits is available from preserved soft parts or carapace design. In *D. oculus* sp. nov., as in other fossil phyllocarid crustaceans, the integumental microstructures are likely to have minimized fluid turbulence both in the water column or in soft, water-permeated sediments. This interpretation finds some support in the fact that the preferential depositional environment of Bolivian phyllocarids is fine, organic-rich, muddy sediment.

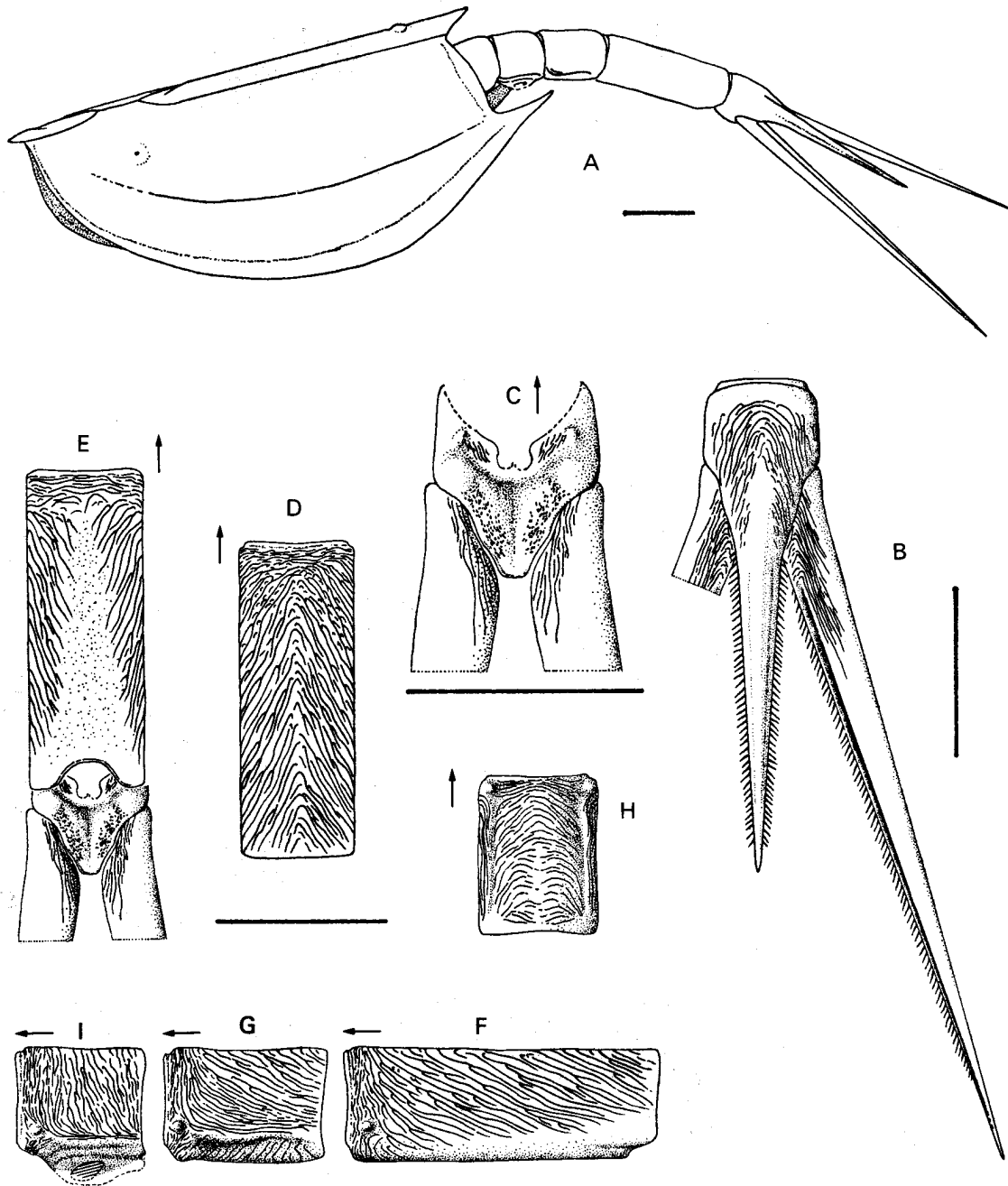
Suprageneric and generic assignment. At the family level, the Bolivian material differs from the *Treatise* diagnosis in that the median dorsal plate is typically narrow, folded longitudinally and roof-shaped in cross section, rather than ‘... slightly bent along dorsal median carina.’ (Rolfe 1969, p. R321). But it is clear that most Devonian species are poorly known, and this species is one of the earliest certain, completely described representatives of the genus (Rolfe and Edwards 1979). The distinction between genera of the family Rhinocarididae remains difficult, especially between *Rhinocaris*, *Tropidocaris* and *Dithyrocaris* (Morzadec and Rolfe 1968; Rolfe 1969; Feldmann *et al.* 1986; Hannibal *et al.* 1994; Racheboeuf 1995). Assignment of the Bolivian form to the genus *Dithyrocaris* follows the interpretation of Hannibal *et al.*: a single mesolateral carina on each valve and a well developed posteroventral spine. The main question remains the significance of the carapace ornamentation which is very different between the type species of *Dithyrocaris* (*Argas testudineus*) and the Bolivian species. One of the most interesting features of the carapace of *D. oculus* is the node developed on the posterior part of the median dorsal plate.

EXPLANATION OF PLATE 3

- Figs 1–6. *Dithyrocaris oculus* sp. nov.; Givetian *Dipleura dekayi* Zone, Lower Sica Sica Formation, Belén section, Bolivian Altiplano. 1, GLAHM 101272; latex replica; enlarged view of the postero-dorsal region of the right valve, showing the dorsal node on the median dorsal plate, the posterior spine-like projections of the dorsal carina, and the ornament of the carapace; × 10. 2–3, GLAHM 101255; latex replica; respectively right and left sides of abdominal somites 5 to 7 and tail piece; note the limb insertion on the 5th somite, and the lateral carina on the 6th somite; × 5. 4–6, GLAHM 101250; latex replica; abdominal somites 5 to 7, and tail piece. 4, enlarged view of the telson showing the ornamentation and the lateral rows of setae insertions; × 8. 5–6, abdominal somites and tail piece, respectively in dorsal and ventral views; × 4.
- Fig. 7. *Dithyrocaris* sp. from Achumani Alto, south of La Paz; GLAHM A2793; latex replica; external mould of the ventral side of a tail piece; × 2.



RACHEBOEUF, *Dithyrocaris*



TEXT-FIG. 5. *Dithyrocaris oculus* sp. nov.; Givetian *Dipleura dekayi* Zone, Lower Sica Sica Formation, Belén section, Bolivian Altiplano. Arrows indicate anterior. Broken lines refer to non-observed, hypothetical outlines. A, reconstruction of the entire exoskeleton. B, reconstruction of the tail piece in dorsal view, mainly from specimens GLAHM 101250 and 101271. C, reconstruction of the ventral side of telson head, from specimen GLAHM 101250. D-F, 7th abdominal somite in dorsal (D), ventral (E), and lateral (F) views, G-H, 6th abdominal somite in lateral (G), and ventral (H) views. I, 5th abdominal somite in lateral view, showing site of left limb insertion. Scale bars represent 5 mm.

TABLE 2. *Dithyrocaris oculus* sp. nov.; Givetian *Dipleura dekayi* Zone, Lower Sica Sica Formation, Belén section, Bolivian Altiplano. Measurements of the abdominal somites, in millimetres. L: length; W: width; H: height; L6:L7: length of the 6th somite versus length of the 7th somite.

	YPFB 8432	AMNH 44696	GLAHM A2792	GLAHM 101250	GLAHM 101253	GLAHM 101254	GLAHM 101255
5th							
L	—	—	—	3	—	—	3.1
W	—	—	—	—	—	—	—
6th							
L	7.6	—	—	4.9	—	—	4.5
W	—	—	—	—	—	—	—
H	6.0	—	—	—	—	—	—
7th							
L	13.1	18	11.5	8.2	11	4.9	8.0
W	4.2	—	—	—	—	—	—
H	4.8	6.8	5.4	4.6	5*	2.4	—
L6:L7	0.58	—	—	0.59	—	—	0.56

Remarks. Valves, abdominal somites, tail pieces and mandibles are assigned to the same species, allowing one of the most complete descriptions of a representative of the genus *Dithyrocaris*. Such an assignment was made possible owing to the preservation, in a concretion, of a carapace with abdominal somites still connected. These somites are identical in morphology, size, and ornamentation to those which are connected with tail pieces in other concretions.

The new available concretion, as well as specimens collected by Branisa, are from the same locality (Belén section), and level (lowermost Sica Sica Formation) as most of the specimens described by Hannibal *et al.* (1994). This fact, added to the description by these authors, as well as our own observations, precludes any doubt about the conspecificity of our specimens and hence about their assignment to the genus *Dithyrocaris*. Hannibal *et al.* (p. 63) compared the Bolivian species with four Carboniferous species: *D. quinni* Copeland, 1967, *D. glabra* Woodward and Etheridge, 1873, *D. granulata* Woodward and Etheridge, 1873, and *D. insignis* Jones and Woodward, 1898, and only one Devonian species: *D. neptuni* (Hall, 1863). These authors stated that the Bolivian specimens '...lack... a distinct "ocular" tubercle (= anterior tubercle)...', although 'Three specimens... seem to exhibit a weakly developed anterior tubercle or tubercles.' Although they questioned the taphonomic or authentic anatomical nature of these tubercles, they considered that the Bolivian species lacks a distinct ocular tubercle, and that this character distinguishes this form from both *D. quinni* and *D. neptuni*. Hence the Bolivian form was assigned to *Dithyrocaris* cf. *D. insignis* due to its produced median dorsal plate and similar size. The good preservation of the 'ocular' tubercle on specimen YPFB Pal 8432, as well as on specimens AMNH 44692, 44693; GLAHM 101261, 101272, raises again the question of comparison at the specific level.

The new species differs strongly from the type species, *D. testudinea* from the Lower Carboniferous of Scotland, by the carapace ornamentation, devoid of strong, oblique, sinuous ridges, by its more elliptical outline, and by the relative length of furcal rami, which are much longer than the telson, whilst they are about the same length in the type species.

Among other species compared by Hannibal *et al.*, *Dithyrocaris oculus* sp. nov. differs from *D. quinni* Copeland, 1967, from the upper Mississippian of Arkansas, in its almost straight (instead of regularly curved) mesolateral carina originating anteriorly in a posterior position with respect to the 'ocular' tubercle. In Copeland's species the mesolateral carina originates at mid-length between the anterior margin and the 'ocular' tubercle (see Copeland 1967, pl. 162, figs 10–12) and the ornamentation is better developed, denser and more prominent on the valve as well as on the abdominal pleonites (pl. 162, figs 6, 12). In *D. quinni*, the denticles point backwards, in contrast to

those of *D. oculus*. They are replaced by irregular curved structures whose anterior edge bounds a depressed posterior area.

Hannibal *et al.* (1994) assigned (with a query) the Bolivian form to the Carboniferous species *Dithyrocaris insignis* Jones and Woodward, 1898 due to its 'less pronounced carapace ornamentation' (p. 63). In fact, *D. insignis* exhibits a carapace surface with both strong linear and reticulate ornaments which are absent in the Bolivian form. According to Jones and Woodward, the '...mesolateral ridge...[is like]...that of *D. tricornis*' (p. 159) which is said to be 'rugose or tuberculate' (p. 171); in the Bolivian form the mesolateral ridge is entirely smooth. Moreover, the Bolivian form differs from *D. tricornis* Jones and Woodward, 1898, in the lack of any punctae, from *D. granulata* Woodward and Etheridge, 1873 in the lack of granulation, and from *D. glabra* Woodward and Etheridge, 1873 in the development of the mesolateral carina as well as by the lack of granulation (see Jones and Woodward 1898). All specimens described and illustrated by Jones and Woodward (1898, 1899) exhibit another peculiar feature: the dorsal side of the posteroventral spine is curved dorsally, whilst in the Bolivian form it is parallel to the carapace midline, in perfect prolongation of the mesolateral carina.

Most interesting is the comparison with Devonian species. *Dithyrocaris neptuni* (Hall, 1863) is a poorly known species, initially described from a tail piece and a fragment of a lateral caudal spine. The illustration of the type specimen (Hall and Clarke 1888, pl. 33, fig. 1) indicates that *D. neptuni* is a very much larger species, but that the relative length of the telson and furcal rami are similar to those of *D. oculus* sp. nov. Stumm and Chilman (1969, p. 60) described *Dithyrocaris* sp. cf. *D. neptuni* (Hall) from the early Givetian Silica Shale of Ohio and indicated that the total length of the species was about 300 mm. Ornamentation (Stumm and Chilman 1969, pl. 5, fig. 4) resembles that of the Bolivian species. Such a peculiar ornamentation has not been illustrated elsewhere, except for another species from the Silica Shale, *Hebertocaris wideneri*, described in the same paper by Stumm and Chilman (1969, p. 63, pl. 6, fig. 4). Although reconstructions exhibit strong morphological differences between *Dithyrocaris* sp. cf. *D. neptuni* and *Hebertocaris wideneri* (compare Text-figs 2 and 3), such a similar ornamentation in two forms, only known by fragments, and from the same stratigraphical level, may be due to an erroneous assignment of carapace fragments. However, *D. oculus* sp. nov. can be distinguished from both forms of the Silica Shale by its smaller size, less developed carapace ornamentation, without spines on the rostral plate as well as on the median dorsal plate, and especially by its smooth as opposed to rugose or cordate mesolateral carina, crossed by the ornamentation.

Dithyrocaris oceani (Hall and Clarke, 1888) from the Portage Group differs from the Bolivian species in its larger size, relatively shorter and curved furcal rami, in the development of coarse granulation in the anterodorsal part of the carapace above the ocular tubercle, and in the straighter lateral carina and ornamentation (Hall and Clarke 1888, pls 32–34).

Dithyrocaris sp.

Plate 3, figure 7

Material. The ventral external mould of a tail piece (GLAHM A2793) from Achumani Alto, south of La Paz, and the anterior part of a tail piece (GLAHM 101283) from Aiquile in the centre of Cochabamba department. Both are of uncertain formation and age.

Comparison. Both specimens assigned provisionally to *Dithyrocaris* sp. differ primarily from *Dithyrocaris oculus* in their much larger size and less elongated telson and furcal rami. The width of the telson head is *c.* 12.5 mm, and its estimated length is *c.* 45 mm, i.e. a length:width ratio of *c.* 3.6. The anterior margin of the ventral platform is 11 mm from the anterior side of the telson. The telson is less elongated than in *D. oculus* where the length:width ratio reaches *c.* 4.5. The furcal rami head is 7.5 mm wide. The furcal rami width versus telson head width ratio is about 0.6. For *D. oculus* the same ratio is 0.5. A tentative reconstruction from specimen GLAHM A2793 gives an estimated length of about 75 mm for the furcal rami, i.e. a length:width ratio of 10. For *D. oculus*,

the length:width ratio of the furcal rami is *c.* 14.5. The ventral side of the telson is more flattened, except for a better differentiated, rounded, narrower longitudinal ridge, than in *D. oculus*. The ornamentation of the telson head, as well as that of furcal rami head, is twice as dense in *D. oculus* as in *Dithyrocaris* sp. Moreover, the flanks of the telson head of *Dithyrocaris* sp. exhibit curved, scale-like lines which have not been observed in *D. oculus*, where the ornament is made of sinuous, oblique lines only. Size and relative proportions of the elements of the tail piece, as well as ornamentation, indicate that this rhinocaridid is a species distinct from *D. oculus*.

PALAEOBIOLOGY AND TAPHONOMY

The postero-dorsal node. Despite its small size and weak relief, this peculiar feature, restricted to the dorsal side of the posterior part of the median dorsal plate, is always well differentiated along the dorsal longitudinal carina, especially in specimen GLAHM A2791. Its location is marked by a weak flexure of the carina in front of the node, and by a stronger flexure behind the node (Text-fig. 3F). The node is symmetrical on both sides of the carina. It is weakly convex and usually slightly pronounced dorsally. Its length does not exceed 1.2 mm, for corresponding height and thickness of 0.8 mm and 0.3 mm respectively. In lateral view, the node is drop-shaped, widening backwards, and smooth in its anterior part. Each side of the node bears minute sub-circular to polygonal punctae which fan out to form a delicate reticulate net which does not cross over the dorsal line. On the internal mould of the carapace, the location of the node is indicated only by a very weak relief without any kind of ornamentation. This fact suggests strongly that the node is not perforated, and that punctae are thinnings of the carapace. The node can be interpreted probably as a sensory organ, possibly for hydrodynamic flow.

Dorsal nodes have been described previously in fossil phyllocarids. Rolfe (1962, p. 916) described three hinge nodes (anterior, median and posterior) on the carapace of *Ceratiocaris* and summarized these observations. The nodes are asymmetrical features developed only on the right valve of ceratiocarines, i.e. phyllocarids whose carapace is devoid of a median dorsal plate. These nodes are smooth '... free of ornament and the carapace striae are distorted or bowed-out in the immediate vicinity of the nodes' (Rolfe 1962, p. 917), although the posterior node shows a circular hole in its centre in both *Ceratiocaris acuminata* Hall and *C. papilio*. Features described in *Mesothyra oceani* by Hall and Clarke (1888, p. 189, pl. 32, fig. 6), and in *Rhinocaris* by Clarke (1893, p. 794), are not homologous in either their morphology or location, to the posterodorsal node of *Dithyrocaris oculus* sp. nov. On the other hand a node exhibiting a similar shape and postero-dorsal location, was also observed on the single left valve specimen of *Kerfornecaris roscanvelensis* Racheboeuf and Rolfe, 1990 of the family Echinocarididae, but as the right valve of this species is unknown the symmetry of the feature cannot be established, and its possible ornamentation could not be described, due to the grain-size of the sediment.

Rolfe (1962, p. 917) considered that the three dorsal hinge nodes on the right valve of *Ceratiocaris* may have acted as hinge clasps, but he wrote that the presence of a circular hole on the posterior node of some species '... may represent some original structure of unknown function.' Although I could not find any similar structures in the literature, it is to be noted that it is situated along the posterodorsal side of the carapace, i.e. opposite to the anteroventral side of the organism, where most sensory organs are located (antennae, eyes, palps, etc.). Moreover, the small sub-circular to polygonal depressions mainly developed backwards, on the posterolateral part of the node, correspond most probably to thinnings of the carapace, although thin sections through the carapace could not be produced. These considerations led the author to interpret the posterodorsal node as a sensor of the surrounding hydrodynamic flow. If the homologous structure and function of the single node described in *Kerfornecaris* could be established, each valve of this genus would have developed a node. This would indicate some kind of parallel tendencies between ceratiocarines and rhinocarines. Further investigations are needed of well preserved phyllocarid material to find similar structures.

Taphonomy. Carapaces of *Echinocaris spiniger* sp. nov. are mostly incomplete. Moreover, they are often broken, exhibiting clean breaks, except for their anterior part which was probably more resistant, due to the development of stout, convex, lobes. Clean breaks, instead of folds or distortion as in *Dithyrocaris oculus* sp. nov. which occurs in the same level, strongly suggest that the carapace was more thickened and mineralized, and hence more brittle. Clean breaks, even in complete exoskeletons of *E. spiniger* sp. nov. (AMNH 43516), are a consequence of diagenetic processes.

The exterior of the left valve of *E. spiniger* specimen YPFB Pal 9290 exhibits sinuous, anastomosing, sub-cylindrical tubes of epizoans. The same specimen shows two very small, juvenile shells of an ambocoelid brachiopod which were possibly attached to the carapace close to the anterior part of the mesolateral carina (Pl. 1, fig. 1). These shells probably belong to the same ambocoelid species as the shell described by Hannibal *et al.* (1994, pp. 60–61), presumably attached to the 7th abdominal somite of specimen AMNH 43516 and re-illustrated herein (Pl. 1, fig. 5). The post-mortem settlement of these epizoans strongly suggests that the carapace of these echinocaridid specimens was not rapidly buried. If the epizoans settled during the life of the organism, this would reflect a nekto-benthic mode of life.

Carapaces of *D. oculus* sp. nov. are found either with both valves still articulated, or as isolated valves. For three of the available articulated carapaces the angle between the two valves varies between 90° and 100°. This is probably not random, and this angular value may correspond to the maximum 'normal' opening of the carapace when the animal was alive. A somewhat similar condition was illustrated for an undetermined late Emsian rhinocaridid from the Massif Armoricain (Racheboeuf 1995, pl. 5, fig. 7). Several other Bolivian specimens, apparently represented by isolated valves, are in fact also articulated carapaces. This is the case for specimens AMNH 44692, GLAHM 101262 and YPFB Pal 8432 which have been prepared to observe the rostral plate. The fact that many concretions appear strongly asymmetrical after breaking, with a 'thin' part yielding the external mould of a valve, and a much thicker part with the corresponding internal mould, strongly suggests that this kind of concretion yields articulated carapaces, and that they break along only one of the two valve planes. In this respect, careful preparation of newly collected concretions would probably allow the collection better data about the taphonomy of the lowermost beds of the Sica Sica Formation.

However, the relatively high percentage of articulated carapaces, added to the discovery of connected abdominal somites and tail pieces, and the occurrence of mandibles associated with carapace remains, indicate a quiet environment. Such preservation strongly suggests that the *D. oculus* remains were buried rapidly. It has to be noted that the carapace of *D. oculus* never shows epizoan tubes, whilst they are commonly developed on the carapace of *E. spiniger*. This may be related to a different mode of life, *Dithyrocaris* being a better swimmer than *Echinocaris* which lived on the sea bottom. Moreover, if carapace and abdominal somite remains show evidence of weak post-mortem distortion, this is directly related to the thin cuticle. Specimens are well preserved, not flattened like most phyllocarids of the Silurian black graptolitic shales, for example. This implies the very early development of the concretions. Such considerations could not be drawn from associated faunal elements such as brachiopods, vertebrate remains, and even complete trilobite exoskeletons occurring in the same level, which are much more heavily mineralized than the phyllocarids.

CONCLUSIONS

Echinocaris spiniger and *Dithyrocaris oculus* can now be listed among the few well-known phyllocarid taxa. The chemical preparation of the moulds of the carapace revealed details of the ornamentation and peculiar, minute features, such as the dorsal node. The latter, which probably represents a sensory organ, developed symmetrically on both sides of the median dorsal plate of the rhinocarine *D. oculus*, and may have homologues in the ceratiocarine genera *Kerfornecaris* and *Echinocaris*, for which symmetrical development remains questionable.

Both Bolivian species described herein are Givetian. That means that the two genera *Echinocaris* and *Dithyrocaris* do not appear in Bolivia earlier than their respective representatives in North

America. From a palaeobiogeographical point of view, the occurrence of representatives of the genera *Echinocaris* and *Dithyrocaris* in the cooler climate of the Malvinokaffric realm is somewhat surprising, because both genera, especially the former, have up to now only been recorded as having tropical to subtropical distribution. The Bolivian representatives of the two genera may have preferred different environmental conditions, i.e. cooler temperatures. In this respect, the overall size of Bolivian specimens from the *Dipleura dekayi* Zone may be of some interest. The largest carapace of *Echinocaris spiniger* is estimated to have been about 50 mm long, whilst that of the North American species *E. punctata* is 90 mm long. The carapace of *Dithyrocaris oculus* apparently does not exceed a length of 50 mm, whilst in North America *D. oceani* may be as large as 140 mm long. Very small representatives of both genera may co-occur in the same beds as these 'giant' North American species (some of them could possibly be juvenile forms). Recent crustaceans generally reach smaller sizes in cool waters than under tropical or subtropical conditions. The relatively smaller size of Bolivian phyllocarid carapaces, compared with North American representatives of the same genera, may possibly be the expression of the impact of cooler water temperature on the growth of these crustaceans.

Acknowledgements. I am grateful to Drs E. N. K. Clarkson (University of Edinburgh), D. A. T. Harper (University College Galway), and an anonymous referee for comments which improved the manuscript. The author is greatly indebted to Mrs Jenna McKnight and Mr John Maret (Collection managers, American Museum of Natural History, New York), for the loan of specimens and for permission to further prepare them. Dr Neil Clark (Hunterian Museum, University of Glasgow) kindly loaned all specimens housed in this collection. Dra Alejandra Dalenz (CTP of YFPB, Santa Cruz, Bolivia) is acknowledged for her help during field trips and for providing collection numbers for the specimens in her charge. Prof. D. E. G. Briggs (University of Bristol) and Drs J.-L. Henry (Université Rennes I), W. D. I. Rolfe (Edinburgh) and J. Vannier (Université Claude-Bernard-Lyon I) are gratefully acknowledged for helpful comments on the manuscript. Photographs were taken by Noël Podevigne, UMR 5565, Lyon. The field work was a part of the 'Siluro-Dévonien malvinocafre' program of the IFEA (Institut Français d'Etudes Andines). This institution and its Director, Christian de Muizon, are gratefully acknowledged for their help and financial support.

REFERENCES

- BABCOCK, L., FELDMANN, R. M., WILSON, M. T. and SUAREZ-RIGLOS, M. 1987. Devonian conulariids of Bolivia. *National Geographic Research*, **3**, 210–231.
- BLIECK, A., GAGNIER, P.-Y., BIGEY, F. P., EDGEcombe, G. D., JANVIER, P., LOBOZIAK, S., RACHEBOEUF, P. R., SEMPERE, T. and STEEMANS, P. 1996. New Devonian fossil localities in Bolivia. *Journal of South American Earth Sciences*, **9**, 295–308.
- BRANISA, L. 1965. Los Fosiles guias de Bolivia. I. Paleozoico. *Boletin of the Servicio Geológico de Bolivia*, **6**, 1–282.
- CLARKE, J. M. 1893. On the structure of the carapace in the Devonian crustacea *Rhinocaris*, and the relation of the genus *Mesothyra* and the phyllocarids. *The American Naturalist*, **27**, 473–801.
- COPELAND, M. J. 1967. A new species of *Dithyrocaris* (Phyllocarida) from the Imo Formation, Upper Mississippian, of Arkansas. *Journal of Paleontology*, **41**, 1195–1196.
- FELDMANN, R. M., BOSWELL, R. M. and KAMMER, T. W. 1986. *Tropidocaris salsiusculus*, a new rhinocaridid (Crustacea: Phyllocarida) from the Upper Devonian Hampshire Formation of West Virginia. *Journal of Paleontology*, **60**, 379–383.
- HALL, J. 1863. On the occurrence of crustacean remains of the genera *Ceratiocaris* and *Dithyrocaris*, with a notice on some new species from the Hamilton Group and Genesee Slate. *16th Report of the New York State Cabinet of Natural History*, Appendix D, 71–75.
- and CLARKE, J. M. 1888. Trilobites and other crustacea of the Oriskany, Upper Helderberg, Hamilton, Portage, Chemung and Catskill Groups. *Geological Survey of the State of New York, Palaeontology*, **7**, 1–236.
- HANNIBAL, J. T., FELDMANN, R. M. and ROLFE, W. D. I. 1994. Phyllocarid crustaceans from the Devonian of Bolivia. In SUAREZ-SORUCO, R. (ed.). *Fosiles y facies de Bolivia*, vol. II Invertebrados y Paleobotanica. *Revista Tecnica Yacimientos Petroleros y Fiscales de Bolivia*, **13–14**, 59–69.

- ISAACSON, P. E. 1977. Devonian stratigraphy and brachiopod paleontology of Bolivia. Part A, Orthida and Strophomenida. *Palaeontographica, Abteilung A*, **155**, 133–192.
- and SABLOCK, P. E. 1988. Devonian system in Bolivia, Peru and northern Chile, 719–728. In McMILLAN, N. J., EMBRY, A. F. and GLASS, D. J. (eds). *Devonian of the World. Volume I, regional syntheses*. Canadian Society of Petroleum Geologists, 795 pp.
- JONES, T. R. and WOODWARD, H. 1898. A monograph of the British Palaeozoic Phyllopoda (Phyllocarida, Packard). Part 3. *Monograph of the Palaeontographical Society*, **52**(243), 125–176, pls 18–25.
- 1899. A monograph of the British Palaeozoic Phyllopoda (Phyllocarida, Packard). Part 4. *Monograph of the Palaeontographical Society*, **53** (248), 177–211, pls 26–31.
- MORZADÉC, P. and ROLFE, W. D. I. 1968. Découverte d'un nouveau Phyllocaride (Crustacés) dans le Dévonien supérieur du Massif armoricain. *Comptes Rendus sommaires de la Société Géologique de France*, **6**, 189–190.
- RACHEBOEUF, P. R. 1995. Silurian and Devonian phyllocarid crustaceans from the Massif Armoricaïn, NW France. *Revue de Paléobiologie*, **13**, 281–305.
- LE HERISSÉ, A., PARIS, F., BABIN, C., GUILLOCHEAU, F., TRUYOLS-MASSONI, M. and SUAREZ-SORUCO, R. 1993. Le Dévonien de Bolivie: biostratigraphie et chronostratigraphie. *Comptes Rendus de l'Académie des Sciences, Paris*, **317**, Série 2, 795–802.
- 1994. El Devónico de Bolivia: bio y chronostratigrafía. *Bulletin de l'Institut Français d'Etudes Andines*, **22**, 645–655.
- and ROLFE, W. D. I. 1990. *Kerfornecaris roscanvelensis* n. g. n. sp.: a new Paleozoic phyllocarid crustacean from the Massif Armoricaïn. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **12**, 735–740.
- ROLFE, W. D. I. 1962. Grosser morphology of the Scottish Silurian phyllocarid crustacean, *Ceratiocaris papilio* Salter in Murchison. *Journal of Paleontology*, **36**, 912–932.
- 1969. Phyllocarida. R296–R331. In MOORE, R. C. (ed.). *Treatise on invertebrate paleontology. Part R. Arthropoda 4*. Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas, 398 pp.
- 1981. Phyllocarida and the origin of the Malacostraca. *Geobios*, **114**, 17–27.
- and EDWARDS, V. A. 1979. Devonian Arthropoda (Trilobita and Ostracoda excluded). 325–329. In HOUSE, M. R., SCRUTTON, C. T. and BASSETT, M. G. (eds). *The Devonian System. Special Papers in Palaeontology*, **23**, 1–353.
- STUMM, E. C. and CHILMAN, R. B. 1969. Phyllocarid crustaceans from the Middle Devonian Silica Shale of northwestern Ohio and southern Michigan. *Contributions from the Museum of Paleontology, University of Michigan*, **23**, 53–71.
- VANNIER, J., BOISSY, P. and RACHEBOEUF, P. R. 1997. Locomotion in *Nebalia bipes*: a possible model for Palaeozoic phyllocarid crustaceans. *Lethaia*, **30**, 89–104.
- WHITFIELD, R. P. 1880. Notice of new forms of fossil crustaceans from the Upper Devonian rocks of Ohio, with descriptions of new genera and species. *American Journal of Science, Third Series*, **19**, 33–42.
- ZITTEL, K. A. 1990. *Text-book of Palaeontology*. Vol. 1. EASTMAN, C. R. (ed.). Macmillan and Co., New York, 706 pp.

PATRICK R. RACHEBOEUF
 U.M.R. 5565 du C.N.R.S.
 Université Claude-Bernard – Lyon I
 U.F.R. Sciences de la Terre
 43, Bd du 11 Novembre 1918
 69622 Villeurbanne, France

Typescript received 19 December 1996
 Revised typescript received 25 March 1997