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Pesquisas em Geociências, 23 (1/2): 41-50, set./dez., 1996.

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Publicado por

Instituto de Geociências

Portal de Periódicos
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Data de publicação - set./dez., 1996.

Instituto de Geociências, Universidade Federal do Rio Grande do Sul, Porto Alegre, RS, Brasil

Pygocephalomorph Crustacea. New Data and Interpretations, with Emphasis on Brazilian and South African Forms

IRAJÁ DAMIANI PINTO & KAREN ADAMI-RODRIGUES

Instituto de Geociências, UFRGS, Caixa Postal 15001 CEP 91500-970 Porto Alegre, RS, Brasil

(Recebido em 10/96. Aceito para publicação em 12/96)

Abstract - New data on Pygocephalomorph Crustacea is provided, together with a historical analysis of previous work on the group. *Pygaspis brasiliensis* Beurlen, 1934 from the Permian Irati Formation of Brazil is redescribed and compared with South African pygocephalomorphs.

INTRODUCTION

Fragmentary fossil crustaceans of the Order Pygocephalomorpha have been recorded from the Permocar-boniferous since the early 1857's and most have been assigned to a single species, by most authors. However, since several quite different taxa are actually involved, the resulting reconstructions are quite incorrect in a number of important respects. This is demonstrated in the present paper in the basis of a historical review of previous work. The confused taxonomic treatment of Permocar-boniferous Pygocephalomorpha has been re-addressed here following the collection of new material from the Irati Formation at Lages, Santa Catarina State, southern Brazil which has provided important new data on Irati Crustacea as well as an improved understanding of the other Pygocephalomorpha as a whole.

CRITICAL HISTORICAL REVIEW

In 1954 the senior author together with A. Cauduro and Y. Sanguinetti (Universidade Federal do Rio Grande do Sul) found a fossiliferous horizon at km 78+800 (now km 90) on the road BR 290 Porto Alegre - Uruguaiana near the Minas do Leão coal mine, Rio Grande do Sul, southern Brazil. At that time the horizon was considered to belong to the Palermo Formation (Pinto, 1955) but it was later assigned to the Irati Formation by Pinto (1957). Fossil material collected at the locality comprised vascular plants, fish scales, an insect and a few crustaceans. In this study of the faunula Pinto (1955) concluded that the crustaceans resembled *Paulocaris pachecoi* Clarke, 1920 from the Irati Formation of the State of São Paulo but lacked the anterolateral spines on the carapace seen in the latter. On the other hand, the Rio Grande do Sul specimens are very similar to *Pygaspis brasiliensis* Beurlen, 1934 from Lages, Santa Catarina State on the basis of the thorax and abdomen. Systematic comparison was complicated by the description of "genal points" in both

Pygaspis brasiliensis and *P. quadrata* by Beurlen (1934, Pl.1, Figs.1 and 2 herein). Such structures are not in fact present in either form, however. Beurlen's misinterpretation was based on lateral breakage of the carapace in some specimens, as established by Pinto (1960: Pl.1, Fig.3 herein) on re-examination of the type material at the Departamento Nacional da Produção Mineral (DNPM) in Rio de Janeiro.

The senior author subsequently collected further crustacean material at the Minas do Leão as well as at the type locality of *P. brasiliensis* at Lages. Pygocephalomorphs in the collections of the University of São Paulo were studied, as well as the types of *Pygocephalus* at the British Museum of Natural History, London and several informative, albeit poorly-preserved, specimens of *Noto-caris* Broom, 1931 kindly loaned by the Alexander McGregor Museum, Kimberley, South Africa. In the resulting publication by Pinto (1971) several problematic aspects of pygocephalomorph systematics were discussed and a redefinition of *Pygaspis brasiliensis* Beurlen, 1934 was attempted. Unfortunately, it was not appreciated at the time that elements of more than one crustacean species were associated in the collections from the Irati, an error which was also made by other workers. As a consequence, a thorough restudy of the Permocar-boniferous Pygocephalomorpha, involving both a review of the relevant literature as well as the re-examination of the type material is required. Such a study is initiated here with a critical review of the literature, a redescription of the Brazilian type and topotype material in particular, and a preliminary discussion of the relationships between the Brazilian and South African pygocephalomorpha taxa. The systematic analysis is based on characters such as the presence of an extended or reflexed abdomen, presence or absence of anterolateral spines and carinae on the carapace, etc. and of necessity reviews these features in the Carboniferous crustaceans which formed the original basis for the Order Pygocephalomorpha.

Pygocephalus cooperi was described by Huxley (1857) from the Carboniferous of England. From Hu-

xley's original illustration (*ibid.*, Pl.13, Fig.1; Pl.1, Figs.4a, b herein), and in contrast to some later representations, it is clear that the abdomen was reflexed ventrally while anterolateral spines were not present on the carapace. *Pygocephalus* showing the same characteristics was subsequently described and refigured by Huxley (1862; Pl.1, Fig.5 herein), Woodward (1907; Pl.1, Fig.6 herein) and Schram (1979; Pl.4, Fig.1 herein). Topotype specimens from the English Coal Measures at the British Museum of Natural History (Pl.4, Figs.2-4) also clearly show the reflexed abdomen and absence of both anterolateral and lateral spines on the carapace. However, an associated carapace (Pl.4, Fig.5) which was also assigned to *P. cooperi* by Schram (1979) clearly belongs to a different genus since both anterolateral and lateral spines are present. Further specimens showing these features are illustrated here in Plate 4, Fig.s. 6a and b.

The genus *Anthropalaemon* with the type species *A. grossarti* was erected by Salter (1861, p.531, Figs.1-4). It possesses anterolateral carapace spines and an extended abdomen (Pl.1, Figs.8a, b). Salter also assigned *Apus dubius* Milne Edwards, 1840 to *Anthropalaemon* (Pl.1, Figs.7a-c). Brooks (1962) in turn synonymised *A. grossarti* with *A. dubius* (Milne Edwards) and placed both within *Pygocephalus*. However, as already indicated, the last genus possesses neither anterolateral spines nor an extended abdomen. Furthermore, *Anthropalaemon grossarti* and *Apus dubius* are not synonymous with each other. The quite different carapace structure as is seen in Pl.1, Fig.7 and 8: length of the rostrum, shape of the anterior margin of the carapace and the presence of lateral carina. Woodward (1907, Fig.1b; Pl.1, Fig.9 herein) figures as *Pygocephalus cooperi*? a pygocephalomorph from the Coal Measures near Rochdale showing an extended abdomen (and no anterolateral spines). Another (*ibid.*, Fig.2; Pl.1, Fig.10 herein) with an extended abdomen and clear anterolateral spines is identified as *Pygocephalus* (*Anthropalaemon*?) *parkeri*. However, these specimens probably do not belong to either of these genera because have abdomen extended (not *Pygocephalus*) and presents gastric spine (no *Anthropalaemon*). Woodward (1907, Pl. 18) also reproduces *Pygocephalus cooperi* from Huxley (1857) as well as a tentative reconstruction of the same species (*ibid.* Pl.18, Fig.4; Pl.1,

Fig.11 herein), showing no trace of anterolateral spines. The reconstruction does not correspond to either of the types or to the remaining figures in his plate and Woodward does not mention upon which specimens it was based.

Brooks (1962) placed *A. parkeri* in synonymy with *P. dubius* but this is unfounded in view of their very different carapace morphology (compare Pl. 1, Figs. 8a,b and 7a-c). Due to the confused state of the early pygocephalomorph literature, and without having topotype material to hand, Brooks (*op. cit.*) in his otherwise wide-ranging and valuable paper unfortunately perpetuated the misinterpretation of the genera *Pygocephalus* and *Anthropalaemon*, and especially that of their Gondwanan relatives. Consequently, the definitions of his new families Pygocephalidae and Notocarididae are open to criticism, as discussed below.

Pinto (1971) drew attention to some of these errors and called into question the synonymy by Brooks (*op.cit.*) followed by Mezzalana (1971), of the clearly discrete and valid genera *Paulocaris* Clarke, 1920, *Liocaris* Beurlen, 1931 and *Pygaspis* Beurlen, 1934.

Brooks (1962) had previously erected the following new families of pygocephalomorph Crustacea:

Family **Pygocephalidae** - carapace with anterolateral spines: *Pygocephalus* Huxley, 1857 together with *Anthracarid*, *Mamayocaris* and *Pseudotealliocaris*, all new genera.

Family **Tealliocarididae** - carapace without anterolateral spines, thoracic sternites with sternal process: *Tealliocaris* Peach, 1908 and *Pseudogalathea* Peach, 1882.

Family **Notocarididae** - abdomen reduced and reflexed under thorax: *Notocaris* Broom, 1931 and *Paulocaris* Clarke, 1920.

However, on the basis of these family definitions *Pygocephalus* would have to be placed within the Notocarididae since it has a reflexed abdomen while lacking anterolateral spines. Likewise, *Paulocaris* with anterolateral spines and an extended abdomen would have to be transferred to the Pygocephalidae.

PLATE 1

- Figure 1 - *Pygaspis brasiliensis* Beurlen, 1934, from Irati Fm. Permian, Lages, S.C., Brasil., 2x.
 Figure 2 - *Pygaspis quadrata* Beurlen, 1934, from Irati Fm. Permian, Lages, S.C., Brasil., 2x.
 Figure 3 - *Pygaspis brasiliensis* Beurlen, 1934, reformed by Pinto, 1960. 2x.
 Figure 4a-b - *Pygocephalus cooperi* Huxley, 1857, from Coal Measures Carboniferous. Medlock, Park Bridge England. 2x.
 Figure 5 - *Pygocephalus* (?) Huxley, 1862, from Coal Shale Carboniferous, near Paisley, England. 2x.
 Figure 6 - *Pygocephalus cooperi* Huxley, 1857, in Woodward 1907 from Coal Measures, Carboniferous, Coseley near Dudley, England. 2x.
 Figure 7 a.b.c. - *Anthropalaemon* (*Palaeocarabus*) *dubius* in Salter, 1861. a-from Lanarkshire; b-from Prestwich Coal brookdale; c-from Ridgeacre Colliery Carboniferous, England. 2x.
 Figure 8a-b - *Anthropalaemon grossarti* Salter, 1861, from Coal Measures Carboniferous, Lanarkshire England. 2x.
 Figure 9 - *Pygocephalus cooperi* (?) Huxley, 1857, in Woodward 1907 from Coal Measures Carboniferous, Sparth, near Rochdale. 2x.
 Figure 10 - *Pygocephalus* (*Anthropalaemon*?) *parkeri* Woodward, 1907, from Coal Measures Carboniferous, Sparth, near Rochdale, England. 2x.
 Figure 11 - *Pygocephalus cooperi* Huxley. An attempted restoration of the male underside Woodward, 1907. 2x.

Since the important but seriously flawed review by Brooks (*op.cit.*) several works on the Pygocephalomorpha of the northern continents have been published which incorporate within *Pygocephalus* composite forms based on what are actually several different genera in terms of the characters already discussed. For example, Brooks (1962, R343, Fig.160-1b) illustrates as *Pygocephalus dubius* the same specimen later designated by Schram (1979, Fig.37; Pl.4, Fig.1 herein) as the holotype of *P. cooperi* Huxley, 1857. The reconstruction of *P. dubius* by Brooks (1962, Fig.160 - 1d; Pl.2, Fig. 1 herein) is based on this specimen, with a reflexed abdomen and lateral spines on the carapace.

The reconstruction of *P. dubius* by Brooks (1962, Fig.160 - 1d; Pl.2, Fig.1 herein) is based on this specimen, with a reflexed abdomen and lateral spines on the carapace. In his review of British Carboniferous Malacostraca Schram (1979) follows Brooks (1962) for the most part in the reconstruction of *P. cooperi* (Schram 1979, Fig.39a), perpetuating earlier errors based on the assumption that the crustaceans assemblage comprised only a single species. In a slightly later review of Upper Carboniferous pygocephalomorphs from the Soviet Union Schram (1980) illustrates *P. cooperi* Huxley, 1857, *P. aisenbergi* (Birshtein, 1966) and *P. dubius* (Milne Edwards, 1840) (Pl.2, Figs.2-4 respectively herein). However, all have anterolateral spines and extended abdomens and therefore cannot belong to *Pygocephalus* as defined by the type species of the genus. Following authors as Brooks (1962) *Anthropalaemon* is erroneously synonymised with *Pygocephalus*, but it is clear that most of the taxa placed by Schram in the latter genus should actually be referred to *Anthropalaemon* instead. Likewise in his paper on Late Paleozoic crustacean communities Schram (1981, Fig.5d) represents *P. cooperi* with extended abdomen and anterolateral spines, additionally referring several other species to the genus *Pygocephalus* on the basis of this character combination which rather defines true *Anthropalaemon*.

The necessity for a thorough revision of the taxonomy of the Pygocephalomorpha is evident. The present paper primarily concerns the revision of Brazilian topotype material; a comparable study of corresponding South African taxa is planned.

Brazilian pygocephalomorpha Crustacea

Repeated reference to South African Permian pygocephalomorphs is necessary when revising the Brazilian forms. When describing *Notocaris* from the Whitehill Formation of South Africa Broom (1931) made the assumption that only a single crustacean genus and species was present in the assemblage, as subsequently did Beurlen (1934) and Pinto (1971) in the case of *Pygaspis* from the Irati Formation of Brazil. Consequently, the definitions of both *N. tapscotti* and *P. brasiliensis* are incorrect, as demonstrated in the latter case by the new material from Lages, Santa Catarina. According to the present authors, and contrary to the earlier reconstructions of Pinto (1971) and Kensley (1975), both *Pygaspis* and *Notocaris* are characterised by the absence of anterolateral spines on the carapace and the presence of a reflexed abdomen; possible synonymy of these genera therefore requires detailed investigation.

The required revision of *Notocaris tapscotti* Broom, 1931, is complicated by the absence of designated holotype or lectotype specimens. The series of specimens illustrated in Broom's paper are currently missing except that represented at plate 1, figure 5. Broom (1931, Pl.1, Fig.1; Pl.2, Fig.5 herein) figures a specimen showing a reflexed abdomen and carapace lacking anterolateral spines. He also states that his account is based on material from the original locality of Woods (1922), all of whose figured specimens (*ibid.*, Pl.6; Pl.2, Figs.6-7 herein) show this combination of characters. These features are therefore taken here as diagnostic of true *Notocaris*, despite the fact that Broom (*op.cit.*, Pl.1, Fig.2) also figured a specimen with an extended abdomen. There is without doubt more than one crustacean species present in the Whitehill assemblage, as observed for the Irati by the present authors.

Paulocaris pachecoi from the Irati was originally erected by Clarke (1920, Pl.3, Figs.1-8; Pl.3, Fig.1 herein) and subsequently refigured by Mezzalana (1954, Pl.9, Figs.1-2; Pl.3, Fig.2a,b herein). The carapace has clear anterolateral spines and a median carina, while the abdomen is extended. Brooks (1962) erroneously synonymised *Paulocaris* with *Liocaris* Beurlen, 1931 (Pl.3, Fig.s.3-4 herein) and *Pygaspis* Beurlen, 1934 (Pl.1, Fig.3 and Pl.3, Fig.8a, b herein) both of which, however, differ

PLATE 2

Figure 1 - *Pygocephalus dubius* (Milne & Edwards 1840), reconstr. by Brooks in Moore 1962, Fig.1d, pg.343 from the British Coal Measures Carboniferous, England. 2x.

Figure 2 - *Pygocephalus cooperi* Huxley, 1857, from Lower Coal Measures, Medlock Park Bridge, Lancashire, England. reconstr. in Schram 1979 fig. 39a and 1980 fig. 3a.

Figure 3 - *Pygocephalus aisenbergi* (Birshtein 1960) in Schram 1980, from Upper Carboniferous, Shcherbinovka Village, Ukraine, Russia. Fig. 3b. 2x.

Figure 4 - *Pygocephalus dubius* (Milne Edwards 1840) in Schram 1980, Fig. 3b from the British Coal Measures, Carboniferous, England. 2x.

Figure 5 - *Notocaris tapscotti* Broom, 1931, from Dwyka Shales, Permian of Kimberley, South Africa. 2x.

Figure 6-7 - *Pygocephalus* in Woods 1922, from the Dwyka Shales, Permian of Kimberley. 2x.

Figure 8a-b - *Pygaspis ginsburgi* Fabre, 1967, from UPPER Dwyka Shales, Permian, South Africa. 2x.

Figure 9 - *Notocaris tapscotti* Broom, 1931. Reconstr. in Pinto 1971, topotype Alexander Mc Gregor Memorial Museum n° 3689e from White Band, Permian, South Africa. 2x.

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markedly from *Paulocaris* in lacking anterolateral spines, carina and extended abdomen.

Beurlen (1934) erected the genus *Pygaspis* from the Irati with two species, *P. brasiliensis* (ibid Fig.1) and *P. quadrata* (ibid. Fig.2). Both were represented with genal points but Pinto (1960; Pl.1, Figs.1-3 herein) subsequently showed that this was not the case, as already mentioned. In his original paper Beurlen also erected the Order Pygaspida and Family Pygaspidae to include the new Irati pygocephalomorphs. Also listed under the Irati Order Pygocephalomorpha were *Paulocaris pachecoi* Beurlen, 1931, *Liocaris huneii* Beurlen, 1931 and *Liocaris angusta* Beurlen, 1931, while *Uronectes brasiliensis* (Clarke, 1920) from Guareí, São Paulo was placed in the Order Anaspidae. *Uronectes* was subsequently transferred to *Clarkecaris* gen. nov. by Mezzalira (1952). Further specimens of *Clarkecaris* from the State of Paraná described by Brito and Quadros (1978) were restudied by Pinto (1985).

Surprisingly, Beurlen (1953) placed two specimens in the genus *Paulocaris* which clearly belong elsewhere. *Paulocaris clarkei* (ibid. Pl.1, Figs.a,b; Pl.3, Fig.5 herein) differs from *Paulocaris* in lacking anterolateral spines and a carina, thus resembling rather his genus *Pygaspis*, while *Paulocaris marianoii* (ibid. Pl.1, Figs. c-e; Pl.3, Fig.6 herein) is quite a different genus which merits revision.

Fabre and Huard (1967, text-figs.2-3; Pl.2, Fig.8a,b herein) presented an extensive, detailed description of *Pygaspis ginsbourgi* from the Whitehill Formation ("Upper Dwyka Shales") of the Laingsburg District, SW Cape, South Africa. They illustrated an enigmatic skeletal element (ibid. Figs.13, 16) which had not been previously identified. However, they mistakenly compared their species with *Pygaspis brasiliensis* Beurlen, 1943 with genal points whose presence in the Brazilian form had already been refuted by Pinto (1960). Surprisingly, however, they did undertake a detailed comparison with the previously established and remarkably similar Whitehill pygocephalomorpha *Notocaris tapscotti*. While the carapace and thorax of *P. ginsbourgi* is similar to Brazilian "*Pygaspis*" (itself possibly a junior synonym of *Notocaris*), the abdomen appears to be quite different; according to the reconstruction of Fabre and Huard (1967, text-figs.2-3) pleural spines are present which are otherwise unknown in either *Notocaris* or *Pygaspis* (cf. Pl.3, Figs.8a, b here

in). Fabre and Huard (*op.cit.*, p. 125-126) make it clear that they adopted the working hypothesis that all their specimens belonged to a single monospecific population. Differences in size and morphology between specimens are ascribed to ontogenetic and taphonomic variation (eg. pattern of deformation), although these authors admit that these views are open to discussion - as has been undertaken in the present paper.

The Order Pygaspida and Family Pygaspidae of Beurlen (1931) were analysed by Secretan (1967) when discussing the true systematic position of *Pygaspis ginsbourgi* Fabre, 1967. Unfortunately, she was unaware that Pinto (1960) has already disproved the existence of genal points in Brazilian *Pygaspis*. She placed the genera *Pygaspis*, *Pygocephalus* and *Notocaris* within the Order Pygaspida of Beurlen, 1931. However for these genera the previously erected Order Pygocephalomorpha of Beurlen, 1930 is still valid and takes precedence. The Family Pygaspidae of Beurlen (1931) would only retain validity over Notocarididae of Brooks (1962) if *Pygaspis* and *Notocaris* are not synonymous, which they actually appear to be.

In his paper on the geology and palaeontology of the Irati Formation Mezzalira (1971) briefly discussed the Syncarida and Eocarida (Pygocephalomorpha). He follows Brooks (1962) in incorrectly synonymising *Liocaris* and *Pygaspis* under *Paulocaris*. He also presents a specimen from Lages, Santa Catarina (IGGSP No 730-7) (ibid. Pl.2, Fig.1; Pl.3, Fig.7 herein) that is erroneously identified as *Paulocaris brasiliensis*; the generic identification is wrong because anterolateral spines and carina are absent, while the shape of the carapace is very different to *Pygaspis brasiliensis*. It probably represents a new species.

Pinto (1971) revised the Pygocephalomorpha, giving at figure 27 a tentative reconstruction of *Pygaspis brasiliensis* Beurlen, 1934 which erroneously depicts an extended abdomen. He also provided an illustration of *Notocaris* based on topotype material showing that it did not have anterolateral spines and that the abdomen was in fact reflexed, Pl.2, figure 9.

Kensley (1975) repeated Pinto's (1971) error of using information from several specimens belonging to different taxa to reconstruct *Notocaris tapscotti*. He mistakenly represents anterolateral spines in *Notocaris*, despite their absence in the specimens illustrated by Broom

PLATE 3

- Figure 1 - *Paulocaris pachecoi* Clarke, 1920, from Irati Form. Permian, Guareí São Paulo State, , Brasil. 2x.
 Figure 2a - *Paulocaris pachecoi* Clarke in Mezzalira 1954, from Irati Fm., Permian, Anhembí, São Paulo State, Brasil. 2x.
 Figure 2b - *Paulocaris pachecoi* Clarke in Mezzalira 1954, from Irati Fm., Permian, Guareí city São Paulo State, Brasil. 2x.
 Figure 3a-b - *Liocaris huenei* Beurlen, 1931, from Irati Fm., Permian, São Paulo State, Brasil. 2x.
 Figure 4a-b - *Liocaris angusta* Beurlen, 1931, from Irati Fm., Permian, São Paulo State, Brasil. 2x.
 Figure 5 - *Paulocaris clarkei* Beurlen, 1953, from Irati Fm., Permian, Paraná Basin, Brasil. 2x.
 Figure 6 - *Paulocaris marianoii* Beurlen, 1953, from Irati Fm., Permian, Dom Pedrito R.G.S. State, Brasil. 2x.
 Figure 7 - *Paulocaris brasiliensis* Beurlen, 1934, in Mezzalira 1971, from Irati Fm., Permian, Lages, S.C. State, Brasil, n°730-1 Coleção IGGSP
 Figure 8a - *Pygaspis brasiliensis* Beurlen, 1934. Holotype DNPM Rio de Janeiro n°3488, Irati Fm., Lages, S.C. State, Brazil. 6.5x.
 Figure 8b - Reconstruction of the same, based on the Holotype only. 6.5x.

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(1931) and in later reconstruction by Pinto (1971). The selection of a lectotype for the *Notocaris* is clearly necessary to avoid further confusion concerning its morphology and systematic affinities.

Reinterpretation of *Pygaspis brasiliensis*

Pygaspis brasiliensis Beurlen, 19934 (emend)
Pl.3 fig.8a and 8b

Holotypus - a ventral view of the specimen n° 3488 of the DNPM - Div. Paleontologia - Rio de Janeiro

Locus typicus - Fazenda Alvim, Lages county, Santa Catarina State, Brazil

Stratum typicum - Irati Formation - Permian of South Brazil

Diagnosis - medium-sized crustacean, carapace with surface papillose ornamented ovoid with maximum width just behind midlength; anterior margin straight, without anterolateral spines; rostrum very short, triangular, slightly longer than wide; lateral spines absent; abdomen reflexed ventrally beneath itself.

Redescription (of holotype specimen) - carapace with surface papillose ornamented ovoid, length 7.4mm, maximum width 7.3mm. Straight anterior margin 4.4mm wide. Posterior margin convex, 4.8mm wide. Abdomen reflexed ventrally, 3.2mm long, and slightly wider than the posterior carapace margin at the junction with the thorax. Total length of specimen 10.6mm. Carapace with short (0.8mm) triangular rostrum. Antennules with three basal segments and two distal flagella, the inner stronger than the outer. Antennae each with a short and a long basal segment, the exopodite forming a flat antennal scale and the endopodite (basal segment not seen) with a long, multisegmented flagellum. All these appendages are broken in the holotype specimen. Round pedunculate eyes apparently present. Mouth parts not clearly preserved, but mandibles, maxillae and maxillipeds can be distinguished. Sternites eight in number, the first triangular and the remainder trapezoidal, becoming progressively larger towards the rear. Pereiopods with two branches: an

endopodite composed of short ischium, merus, carpus and dactylus; an exopodite with three basal articles and an elongate flagellum which appears to be incompletely subdivided, with full rings formed only at the margins. In the holotype, several pereiopods are incomplete or absent. Abdomen reflexed ventrally beneath itself showing five pleonites on one side and a circular telson apparently turned over in the middle of the telson tip a triangular spine.

CONCLUSIONS

1. The association within a single sample of isolated skeletal elements (carapaces, abdomina, antennae, legs etc) does not preclude the possibility that more than one species, or even genus, of crustacean is involved.
2. The type localities of *Pygaspis brasiliensis* and *Notocaris tapscotti* have also yielded additional crustacean genera, and the same may apply to that of *Pygocephalus cooperi*.
3. *Pygocephalus cooperi* Huxley, 1857 does not have anterolateral spines and the abdomen is reflexed beneath itself.
4. *Anthropalaemon* Salter, 1861 is a valid genus characterised by the presence of anterolateral and gastric spines, the absence of hepatic spines, the abdomen is extended.
5. *Notocaris* Broom, 1931 lacks anterolateral spines as well as gastric and hepatic spines; the abdomen was reflexed ventrally. The reconstruction of *Notocaris tapscotti* Broom, 1931 by Kensley (1975) does not correspond to the type series of Broom (1931) and did not represent the genus or the species.
6. *Pygaspis brasiliensis* has a reflexed abdomen and anterolateral spines are not present on the carapace. Once a lectotype of South African *N. tapscotti* is selected, the question as to whether *Pygaspis* is a junior synonym of *Notocaris* can be resolved. In turn this will also settle the validity of the Family Pygaspidae versus Notocarididae.

PLATE 4

All figures in natural size

Figure 1 - *Pygocephalus cooperi* Huxley, 1857, in Schram 1979 fig.37 Holotype L 10221 from the Coal Measures, Carboniferous, Medlock Park Bridge, England.

Figure 2 to 4 - *Pygocephalus cooperi* Huxley, 1857, by Pinto from Coal Measures, Carboniferous, Medlock Park Bridge, England. Topotypes of the British Museum of Natural History, London.

Figure 2a - Ventral view.

Figure 2b - Carapace without antero-lateral or lateral spines. Abdomen reflexed under itself and thin pleonites are seen;

Figure 3a - Dorsal view

Figure 3b - Ventral view showing the caudal elements.

Figure 4 - Caudal tail showing telson, uropodes, furcal lobes and median spine in the reflexed abdomen.

Figure 5 - Gen. et sp. Indeterminate. *Pygocephalus cooperi* Huxley, 1857, in Schram 1979, Topotype I 13948 of the British Museum of Natural History from Coal Measures Carboniferous, Medlock Park Bridge, England. Photos by Pinto.

Figure 6 - Gen. et sp. indeterminate, Topotype n° I 13948, a dorsal view, b ventral view of the British Museum of Natural History from Coal Measures Carboniferous, Medlock Park Bridge, England. Photos by Pinto

7. On the families created by Brooks (1962), neither the Pygocephalidae nor the Notocaridae are valid according to the morphological criteria of Brooks himself and therefore require redefinition.
8. A thorough revision of the genera *Pygocephalus*, *Notocaris* and *Pygaspis* together with associated Crustacea is necessary for a proper systematic understanding of the extinct Order Pygocephalomorpha.

Acknowledgments - Many thanks to Prof. Dr. John Almond of the Geological Survey of South Africa for his kind comments and suggestions on this paper, to Dr. Ivone Purper for patiently typing of the manuscript, to Mr. Luiz Flavio Pereira Lopes for the reproduction of the photographs, to FAPERGS (Fundação de Amparo à Pesquisa do Estado do Rio Grande do Sul) and CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico do Brasil) for their continuous support to the authors researches.

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