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### The Species of *Pleuroxus* and of Three Related Genera (Anomopoda, Chydoridae) in Southern Australia and New Zealand

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ABSTRACT. Two new chydorid cladoceran genera, *Planicirclus* (n.gen.) with one species *Planicirclus alticarinatus* (n.sp.), and *Plurispina* (n. gen.) with two species, *Plurispina chauliodus* (n.sp.) and *P. multituberculata* (n.sp.), are described from south-western Australia. The status of the chydorid genus *Pleuroxus* in southern Australia and New Zealand is reviewed, with two new species described: *Pleuroxus foveatus* (n.sp.) from south-western Australia, and *P. helvenacus* (n.sp.) from New Zealand. The European species *Pleuroxus aduncus* (Jurine), previously identified from the region, is described, and shown definitely not to occur there. *Pleuroxus hastirostris* Sars and *P. inermis* Sars are redescribed, as is *Archepleuroxus baylyi* Smirnov & Timms. Four other species of *Pleuroxus* described from southern Australia are considered *nomina dubia*. All eight recognised taxa appear to be endemic to the region. Marked differences between the *Pleuroxus* fauna of eastern and western Australia provide evidence for adaptive radiation. It is likely that a comparable high degree of endemicity will be found in other chydorid groups.

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Cladocerans, small branchiopod crustaceans, are predominantly freshwater in affinity. They are widely distributed in Australasian inland waters, but systematic and ecological studies of them have been few. A major difficulty has been the lack of taxonomic keys to the Australasian fauna, compounded by indiscriminate use of available (northern hemisphere) authoritative references, e.g. Ward & Whipple (revised by Edmondson, 1963) or Pennak (1978). More recently, an appropriate level of resolution of Australian daphniid cladocerans has been achieved by scanning electron microscopy (SEM), e.g. *Simocephalus* (Dumont *in* Smirnov & Timms, 1983) or electrophoretic methods, e.g. *Daphnia carinata* (Benzie, 1986). However, most families of Australasian Cladocera remain poorly resolved.

Identifying species of Chydoridae, in particular, presents problems. If one were concerned with one region, I believed he could define the species easily enough and put unique names on them, but if he were concerned also with equivalence or conspecificity between regions, then the matter becomes much more difficult. Most generic names have had no formal description in the literature, and species names have been transferred from one continent to another. The result is that many species throughout the world are improperly named, and many genera are not monophyletic.

In questioning widely accepted cosmopolitanism in cladocerans (Frey, 1982), I had become convinced that the present distribution of chydorid species in the world was likely influenced in part by the breakup of Gondwana. To investigate this hypothesis I collected intensively in Australia and New Zealand in 1986 to 1987. From more than 400 samples collected, and from almost as many collected previously by other scientists, which I was privileged to examine, I obtained many exceptional populations of various chydorids. The fauna of New Zealand was investigated first, being much less extensive than that of Australia, and *Pleuroxus* was the first genus examined, because only a single species, *P. hastirostris*, had been described from that country.

*Pleuroxus hastirostris* was readily defined, but the New Zealand material contained a second taxon which seemed to resemble *Pleuroxus jugosus* Henry from Australia, as treated by Smirnov & Timms (1983). Deciding the identity of this second taxon thus required a detailed comparison with the Australian taxon, and here is where the problems began. The *Pleuroxus jugosus* of Henry is represented by only a holotype, which is an immature specimen that does not show many of the characters needed for identification. Moreover, Smirnov & Timms (1983) in their expanded description of the taxon mistakenly used a species from a different genus (described in this paper). Additionally, populations from Western Australia differed significantly from the accepted morphology of *Pleuroxus*. It was difficult at first to define the populations by species, much less put names on them.

The final outcome is that two new genera and five new species are described in this paper, with redescriptions of four other taxa described previously. Pleuroxus aduncus from Europe is included to provide a contemporary description of the taxon for comparison with the Australian taxa, or with populations from other parts of the world that presently are named Pleuroxus aduncus. Although claimed to occur in Australia, it does not (P. inermis is closest to it), and neither of the two New Zealand species occurs in Australia. No species named on other continents are present. Thus, here is still another example of non-cosmopolitanism among chydorids where cosmopolitanism previously had been thought to exist. There is a very high rate of endemism, even higher than that indicated by Smirnov & Timms (1983). It seems certain that other new taxa will be discovered, particularly in south-western Western Australia, by collecting in unique kinds of aquatic habitats, including seasonal, weakly to moderately saline, extremely shallow, or those having a variety of other restrictive features.

What these studies indicate is that when examined in detail, the related taxa of a region differ kaleidoscopically in many morphological characters, making it difficult to decide the limits of the species. Australia, because of its very large number of endemic taxa, may be different from the other continents in the amount of such differentiation, but as this is the first such study conducted on any continent, one cannot be certain. It may be that other continents will show a corresponding amount of morphological differentiation among closely related species.



**Fig.1.** Length-frequency distributions by stage of females and instars of males of the populations of the various taxa considered in this study. *Pleuroxus inermis* and *Pleuroxus foveatus* are each represented by several different populations. The other seven taxa are each represented by a single population, although the two taxa from New Zealand – *Pleuroxus hastirostris* and *Pleuroxus helvenacus* – have a few individuals from collections by other persons available for comparison and for including in the descriptions. The early frequency peaks of parthenogenetic females are not labelled specifically, but it should be apparent that they correspond to the prereproductive instars I and II recognised in other chydorids.

Almost 16% of the samples collected in Australia contained one or another species of *Pleuroxus* or related genera, mainly *Pleuroxus inermis*, but only two out of 157 samples collected in New Zealand. Some of the best populations available, which yielded the new species and genera from Western Australia, are from samples collected by I.A.E. Bayly and R.J. Shiel.

#### Methods

My personal samples were collected in the littoral region with a pole-mounted net of 120 µm Nitex, the mouth of which was covered with 5 mm mesh bronze screen to keep out large objects. The samples were preserved immediately with commercial formalin (roughly 40% formaldehyde) containing about 4% sucrose by adding 2 to 4 ml to a 125 ml sample, giving a final concentration of about 1% formaldehyde. The collections of Bayly were made with an about 200 µm-mesh dip net and those of Shiel with a 53 µm-mesh Birge cone net. All samples are stored in weak formalin, which seems the best preservative for retaining the exoskeleton and internal organs in good condition. In the laboratory the samples were inventoried at 25x stereo magnification for the various animals they contained. For the anomopods, notes were made on abundance, presence of gamogenetic stages, and any noteworthy details of morphology. The information on the inventory cards enables the best samples for any species to be identified for further study.

For the samples used in this study, aliquots were placed in a petri dish, systematically examined at 25x, and all specimens and exuviae of the Pleuroxus species were removed to a depression slide, where they were equilibrated with glycerol. These specimens then were mounted temporarily in glycerol, about 40 per coverslip, for measurement of length and for camera lucida drawings of animals and their parts. Fresh exuviae are the best material for revealing the details of the head appendages, trunklimbs, postabdomen and claws, and details of shell sculpturing and setation. The individual parts are dissected away from one another and then mounted either in glycerol or polyvinyl-lactophenol (PVL) stained with lignin pink. Sometimes intact specimens must be dissected for shape of the rostrum and other details of structure, particularly when good exuviae are not available. Specimens from samples collected by other persons were handled in the same manner.

Specimens and their parts were examined on a Wild M20 compound microscope with phase-contrast optics. Measurements were made with an ocular scale calibrated against a micrometer slide (0.1 and 0.01 mm units). Drawings were made with a Wild binocular *camera lucida* calibrated against the same micrometer scale.

For the SEM photographs, specimens were selected, dissected if necessary to reveal the postabdomen, trunklimbs, and head appendages, and then 'washed' with a fine pipette to remove any loose detritus. Most chydorids are clean when alive. If they are rinsed thoroughly in the net to remove particles smaller than about 100  $\mu$ m, they generally provide excellent material for SEMs. If they are captured with a finer net, or not washed adequately, the fine material gets between the shells and also, over time, becomes firmly fastened to the outside of the animal, where it cannot be removed, at least easily, by detergents. Even weak sonication is too drastic a procedure for chydorids, resulting in the loss of many of the setae.

Documentary specimens, including holotypes and paratypes, placed in museums were mostly mounted in glycerine jelly, with the cover glasses supported by small squares of plastic. Exuviae and dissected parts of specimens were mounted in PVL/lignin pink. All slides were sealed either with Zut or Glyceel to protect the specimens and to curtail loss of water from the PVL mounts.

Specimens of taxa from Australia or New Zealand described by Sars or Henry were borrowed from the Sars Museum in Oslo and the Australian Museum in South Sydney (see Table 1). All tables referred to in this paper are included in the Appendix. The following abbreviations for institutions are used: AM – Australian Museum, Sydney; BM(NH) – British Museum (Natural History), London; NMNZ – National Museum of New Zealand, Wellington; USNMNH – United States National Museum of Natural History, Washington.

#### Historical Resumé of Previous Studies

Table 1 lists all the *Pleuroxus* and *Pleuroxus*-like taxa that have been claimed to occur in Australia or New Zealand, including the new taxa from the present study. Four of the first six species claimed to occur in Australia and New Zealand were described from other continents. Of these, P. denticulatus, P. similis and P. laevis are not considered in this paper because they differ so markedly from all the other species. Besides, since they were described from other continents, a detailed comparison would need to be made between type populations and populations from Australia presently bearing these names. For P. laevis this should be relatively easy, as there is now a detailed description of the taxon in the literature (Frey, 1988). Two other taxa were described by Sars (1896, 1903), one species each from Australia and New Zealand. Smith (1909) later described a new species from Tasmania, and Henry (1918, 1922) described five species (three in the genus Chydorus) from the Sydney region, all of which tended to be ignored by subsequent workers because of the poor descriptions and illustrations. Her taxon Chydorus jugosus, although closely related to the two species here placed in a new genus, cannot be identified from the single immature specimen available. Henry's Pleuroxus reticulatus apparently involves two different taxa. neither of which is in the genus Pleuroxus. Smirnov & Timms (1983) erected the new genus and species Archepleuroxus baylyi but kept everything else in

much the same unresolved state. They synonymised Henry's species with *Pleuroxus aduncus* and *Pleuroxus similis*. The present paper includes *Pleuroxus aduncus* described from Europe but does not include the other three taxa described from other continents. It is suggested, though, on the basis of past detailed studies, that what occurs in Australia will be found to resemble the strict taxa only superficially when adequate comparisons are made.

#### **Taxonomic Descriptions**

#### Pleuroxus Baird

#### Pleuroxus aduncus (Jurine)

#### Figs 2-47

Monoculus aduncus Jurine, 1820: 152-153, pl.15, figs 8,9. [See Smirnov (1971) for the numerous subsequent and often confusing entries in the synonymy].

**Remarks.** The conceptual understanding of this species is similar to that of many other chydorids described earlier. Jurine (1820) has a very incomplete description of the taxon, accompanied by two small figures that are reasonably accurate but inadequate for present-day needs. Moreover, none of the specimens Jurine used are still extant. He only collected the taxon from Châtelaine, France.

Since that time, many workers have found populations resembling P. aduncus on all continents except Antarctica and have either given them the same name or have described them as new species or varieties. Smirnov (1971) aggregated seven species and four varieties with P. aduncus, recognising four subspecies, some of which (such as P. aduncus laticaudatus) do not seem to belong to the same species. Later (in Smirnov & Timms, 1983) he synonymised three more species with P. aduncus. In this latter paper he stated that P. aduncus "... is a polymorphic species or a complex of related forms...", based in part on an analysis by Harding (1955). Hence, to define the taxa that occur in Australia, which include *P. aduncus* and *P. inermis*, the latter having been synonymised with *P. aduncus* (Smirnov, 1971) but later (Smirnov & Timms, 1983) re-established as a separate species, it is necessary first to define the European taxon more closely to facilitate comparisons.

**Material examined.** The species was described from France, but all our collections are from northern Europe. However, as only one *aduncus*-like species is claimed to occur in Western Europe, the population from Denmark used here can be considered typical for the taxon. The sample selected out of the many available is 3004 from Langemose, which is located between 4 and 5 km on the road from Helsingør to Helsinge, Sjælland, Denmark, collected 23 October 1971. It yielded about 70 specimens, including ephippial females and instars II and III of males.

**Disposition of specimens.** One slide each of a parthenogenetic female, an ephippial female, an instar-II male, and a mature male, mounted separately in glycerine jelly, have been deposited in the following museums. The numbers given are the catalogue or registration numbers of the specimens.

	AM	NMNZ BM(NH)		USNMNH	
parthenogenetic	P39453	Cr. 6412.	1989.600	242113	
female					
ephippial female	P39454	Cr. 6413	1989.601	-	
instar-II male	P39455	Cr. 6414	-	-	
mature male	P39456	Cr. 6415	1989.602	242113	

Diagnosis. Longer than high. Dorsal margin broadly arched, slightly concave near posterior-dorsal angle; 0-4 teeth (most commonly 2) at posterior-ventral angle; posterior margin short, distinctly convex; ventral margin with pronounced ventral bulge in anterior half; about 10 curved striae in anterior-ventral portion of shell. Rostrum elongate, bluntly tipped. Labral plate large; tip attenuated, narrowly rounded. Postabdomen with 7-10 denticles along postanal margin, each usually accompanied by 1 or more setae, forming clusters that distally are oriented obliquely, proximally are parallel to margin. Abdominal setae long, reaching about halfway in anal groove. Eight setae on antennae; one of terminal setae on endopodite much shorter than others, seta from basal segment very long; terminal spines very short, indistinct. Rounded process extending backward from base of antennule. Males II and III more elongate than females; maximum height at or slightly in front of ventral bulge; postabdomen of mature male tapered distally to base of claws, provided with diagonal groups of setae at margin, a few distal setae thickened into respectable denticles; genital pore terminal near base of claws; seemingly only 1 basal spine on claw.

Parthenogenetic female. Shape and shell (Figs 2-6, 33, 38, 39). Maximum dorsal curvature posterior to ventral bulge; slight concavity just before posteriordorsal angle; posterior margin short, weakly and evenly convex, only about one third total height of animal; 0-3 denticles on shell [0,2 (2); 1,1 (3); 1,2 (10); 1,3 (4); 2,2 (13); 2,3 (3); 3,3 (1); 1 immature female with 4 on one side], when multiple tending to occur more on posterior margin than at posterior-ventral angle; distinct line closely paralleling posterior margin, provided with fine spinules beginning immediately after denticles, continuing well toward posterior-dorsal angle (Figs 4, 33, 38, 39); ventral margin with 84 (range 79-89, n=19) marginal setae, including about 10 directed inward along anterior margin (Fig.6); anterior-ventral quarter of shell with about 10 irregularly curved striae; generally a slight bulge in lateral outline each over eye and ocellus.

*Head.* Headshield elongate, narrowed and rounded posteriorly (Fig.17); postpore distance (from posterior headpore to margin of headshield, hereafter PP) about 3 times interpore (IP) distance (n=5); minor pores about

one pore diameter apart; rostrum tapered to bluntly rounded tip (Fig.35); eye somewhat larger than ocellus, which is closer to eye than to tip of rostrum; no markings on head.

Antennule (Figs 2-4, 15, 35). Elongate, slightly curved,

tapering distally; base provided with round-tipped projection extending backward (Fig.15); 9 aesthetascs, one thicker and longer than others; antennular seta arises about one third to two fifths from tip, longer than any aesthetasc; all aesthetascs terminate well before tip of



Figs 2-18. *Pleuroxus aduncus* (Jurine, 1820). All specimens are females from Frey sample 3004 (Langemose, Denmark, 23 Oct. 1971). 2. instar-II female; 3. mature parthenogenetic female; 4. posterior margin of shell and posterior-ventral angle of mature parthenogenetic female; 5. ephippial female; 6. shell of parthenogenetic female; 7-14. labra of parthenogenetic females; 15. antennule; 16. antenna; 17. headshield; 18. postabdomen and postabdominal claw.

rostrum.

Antenna (Figs 16, 35). Formula: 0-0-3(1)/1-1-3(1). Expopodite with 3 almost equally long terminal setae;

endopodite also with 3 terminal setae, one much shorter than other 2; middle segment with a seta as long as distal setae; basal segment with a more slender but still long



Figs 19-31. *Pleuroxus aduncus* (Jurine, 1820). All specimens are from Frey sample 3004 (Langemose, Denmark, 23 Oct. 1971). 19. trunklimb I of parthenogenetic female (ODL2 not visible); 20. part of trunklimb II of parthenogenetic female; 21. instar-I male; 22. mature male; 23. shell of mature male; 24. part of trunklimb I of instar-II male (MS', anlage of male seta on IDL); 25. part of trunklimb I of mature male; 26, 27. postabdomen of instar-II male; 28. postabdomen of mature male, showing the attenuation toward the claws, and the marginal setae arranged mostly in rows oriented diagonally to margin; 29. rostrum and antennules of instar-II male; 30. rostrum of mature male; 31. antennule of mature male, showing the long, unfeathered male seta (M) and the 12 unequal aesthetascs.

and functional seta; small, inconspicuous terminal spine on each branch, exopodite spine slightly larger; spine from basal segment very small, obscure.

*Labrum* (Figs 7-14). Keel broadly expanded, convex anteriorly, sometimes slightly concave near tip, which is narrowed and rounded; posterior margin concave; posterior angle rather narrow, generally about 90°.

Trunklimb I (Figs 19, 34, 44). Two outer distal lobe

(ODL) setae, one very short and often not visible; 3 inner distal lobe (IDL) setae, 2 long, provided with row of short setules along distal segment, shortest barely as long as basal segments of other two. Middle seta of middle group of corm setae much the longest; all 3 accessory setae well developed; lateral seta very thin and fragile, as long as IDL setae (Figs 19, 34).

Trunklimb II (Fig.20). Usually 8 setae in gnathobasic



Figs 32-39. *Pleuroxus aduncus* (Jurine, 1820). All specimens are from Frey sample 3004 (Langemose, Denmark, 23 Oct. 1971). 32. ephippial female; 33. posterior-ventral angle of mature male; 34. trunklimb I of ephippial female (LS, lateral seta; ODL2, short, unfeathered seta on ODL); 35. tip of rostrum, labrum, and head appendages of ephippial female; 36, 37. postabdomen and claws of parthenogenetic female; 38, 39. posterior-ventral angle with tooth and inner side of posterior margin of shell of ephippial female.

filter comb (specimen drawn has 9); first 3 scraping spines subequal in length, much shorter than spine 4, all provided with small, virtually uncountable marginal setules along distal segment.

*Trunklimbs III-V.* Eight, 6 and 4 gnathobasic filter setae, respectively; 7, 7 and 4 feathered exopodite setae, respectively. Other morphology quite indistinguishable from that of other *Pleuroxus* species.

*Postabdomen* (Figs 18, 36, 37). Preanal and anal portions subequal in length, both shorter than postanal portion; preanal portion with transverse expansion beginning shortly anterior to preanal angle; anal groove concave; postanal angle rounded; dorsal postanal margin weakly convex, tapering distally to rounded distal angle; ventral margin with 2 (possibly 3) transverse crescents of spinules. About 7-10 groups of marginal setae,



Figs 40-47. *Pleuroxus aduncus* (Jurine, 1820). All specimens are mature males from Frey sample 3004 (Langemose, Denmark, 23 Oct. 1971). 40. side view; 41. head end, showing rostrum, labrum, and antennule; 42. rounded rostrum; 43. head end of dissected specimen, showing rostrum, antenna, and antennule, the latter with a long, unfeathered male seta (M), antennular seta (AS), and unequal aesthetascs; 44. trunklimb I (MS, male seta; LS, lateral seta); 45. postabdomen; 46. distal end of postabdomen and claws (GP, genital pore); 47. postabdominal claws, showing sigmoid shape and irregular shape of longer basal spine.

distalmost member of each group thickened, denticlelike; several unthickened setae distal to last denticle around tip of postabdomen; anal groove bordered by about 5 successive rows of setules; single row of crescents of spinules along postanal and distal half of anal margins; a few more crescents near preanal angle. Abdominal setae long, reaching to about mid-anal groove, or slightly beyond, when extended.

*Postabdominal claw* (Figs 18, 37). Long, relatively straight; dorsal and ventral margins weakly and regularly curved; dorsal margin with row of fine spinules; 2 basal spines, longer one curved outward, longer than basal width of claw (Fig.37); shorter one straight, very slender, about half as long.

**Ephippial female** (Figs 5, 32). Laterally more compressed than parthenogenetic female; dorsal margin thickened in typical fashion; marked change in curvature between shell and headshield; headshield more elongate and narrowed, with sharp triangular expansion at top of slough line; ephippium with only light pigmentation; no detectable patterning or sculpturing of shell of ephippium; shell flaps narrowly attached to ephippium posteriorly, easily lost.

Male (Figs 21, 22, 40). In instar-II, rostrum shortened (compared with female) and broadly rounded at tip (Fig.29); postabdomen similar to female except for irregular ventral margin and bulge near tip ventrally to accommodate genital pore (Figs 26, 27); trunklimb I with typical setae and 2 anlagen of setae (Fig.24) that become functional in instar-III (Figs 25, 44); short anlage of male setae on antennule. In instar-III (= mature), rostrum still shorter, tip broader, truncately rounded (Figs 30, 42); antennule with a long seta, located slightly proximal from antennular seta (Figs 31, 41, 43); 12 aesthetascs (although another antennule seemed to show only 9), one of which is longer and stouter than others; copulatory hook with 3 curved crescents at inner tip (Fig.44); postabdomen more slender than in female, tapered postanally to base of claw, provided with about 7 oblique rows of spinules (Figs 28, 40, 45); genital pore terminal near ventral margin (Figs 46, 47); claw shorter and somewhat stouter than in female, somewhat sigmoid in outline, and seems to have just a single basal spine (Figs 28, 46, 47); ventral margin irregular.

**Length.** Females: overall 0.34-0.60 mm (n=72); instar-I 0.34-0.37 mm (n=11); instar-II 0.42-0.46 mm (n=10); mature 0.48-0.60 mm (n=35); smallest with eggs 0.48 mm; ephippial 0.52-0.60 mm (n=4). Males: instar-II 0.39-0.42 mm (n=4); mature 0.42-0.46 mm (n=8).

**Comments.** Thus, *P. aduncus sensu stricto* is considerably less high than long, with both posteriordorsal and posterior-ventral angles well developed, the former accentuated by a slight concavity nearby in the dorsal margin and the latter by none to four conspicuous teeth, which occur at the angle, or, if multiple, low along the posterior margin. The ventral margin is not straight but has a marked bulge or expansion anterior to the middle. The shell is smooth except for the ten or so curved striae near the anterior end. The postabdomen has thin denticles, which are always multiple. The labrum is quite broad and the tip not strongly attenuated. The preanal margin of the postabdomen has only a very short section near the anus that is not expanded laterally. The postabdomen of the male is strongly tapered postanally and is provided with seven or eight mostly oblique rows of setae. The postpore distance of mature females is only about three times the interpore distance. There is no keel on the head or shell.

Pleuroxus aduncus sensu stricto has a pattern of morphology not seen in any population from Australia. The claim that P. aduncus occurs in this part of the world must be based on an inadequate comparison of the populations from Australia and Europe, using only a few general characters readily visible, and guided by the mistaken belief that chydorids are distributed readily by their resting eggs so that the same species can occur easily on different continents.

#### Pleuroxus inermis Sars

#### Figs 48-147

- Pleuroxus inermis Sars, 1896: 31-35, pl.5, figs 8-9.–Haase, 1903: 150, fig.6.–Sars, 1916 (Africa): 342-343, pl.41, figs 2, 2a-2b.–Henry, 1922: 44-45.–Smirnov & Timms, 1983: 25, fig.24.
- Pleuroxus aduncus.-Smirnov, 1971: 221 (not Monoculus aduncus Jurine, 1820).

**Remarks.** Sars named this species *Pleuroxus inermis* because he thought the taxon lacked a tooth (or teeth) on the shell, the presence of which is characteristic of most other species of Pleuroxus. However, a tooth is present on many specimens, even those in the Sars samples. It is generally very small, arising submarginally, and often oriented along the margin of the shell so that frequently it is visible with great difficulty using standard optics, although more readily visible with phase optics. Its presence is variable. Frey sample 7961 from South Australia has almost every individual with a small tooth, whereas Frey sample 8026 from Western Australia has only the occasional individual with a tooth. Such differences may have resulted from at least partial isolation of populations in Western Australia from those in the east.

This seems to be the commonest and most widespread species of *Pleuroxus* in the southern part of Australia. It is relatively small, highly arched but unkeeled, without shell markings except for eight to ten curved striae roughly paralleling the anterior margin of the shell. It has either one minute tooth on the shell or none, and it has the postabdomen tapering and the postanal margin provided with about 12 long, slender denticles, of which the distal ones are all single and the proximal ones multiple. Sars (1889) at first thought this species was the same as King's (1853) *Chydorus augustus*, but later he decided King's species was *Chydorus globosus* (Sars, 1888). He considered the taxon closely related to *Pleuroxus aduncus* of Europe but separated from it by a number of distinctive characters, which he specified. Smirnov (1971) considered

*P. inermis* a synonym of *P. aduncus*, but then later (Smirnov & Timms, 1983) restored it to full species status. It is really quite different from *P. aduncus*, as detailed at the end of this section, and should not be confused with it.



**Figs 48-63**. *Pleuroxus inermis* Sars, 1896. All specimens are parthenogenetic females from Sars sample F4139, raised from dried mud collected by Th. Whitelegge near Waterloo, NSW, about 1892. 48. side view of LECTOTYPE; 49. trunklimb I (ODL2, unfeathered, short ODL seta; IDL3, third seta on IDL, unfeathered); 50. antenna; 51-53. postabdomen (lateral crescents of setules not discernible in Fig.52, which is from LECTOTYPE); 54. postabdominal claw; 55-62. labra; 63. antennule (number of aesthetascs could not be distinguished).

All the records of this taxon are from Australia, except for Sars' 1916 record from South Africa. However, Sars' figure of the taxon in this paper does not match the shape of P. *inermis* from Australia, being less high, and hence may be a different taxon.

**Material examined.** 1. Sars' slides: a. F9671, Victoria, 15 specimens, all of which are in small bits of mounting medium. The specimens are not useable without remounting; b. F9672, Bourke Street, Waterloo, Whitelegge, 5 specimens in balsam, all good. One has been selected as the LECTOTYPE of the taxon; c. F11731,



**Figs 64-78.** *Pleuroxus inermis* Sars, 1896. All specimens are from Frey sample 8026 from a natural pond near Waroona, WA, collected 20 Nov. 1986. All figures are of parthenogenetic females except Fig.66. 64. side view; 65. shell of parthenogenetic female; 66. ephippium, showing dimples resulting from contraction of brood pouch lining; 67. trunklimb I; 68. gnathobasic portion of trunklimb III; 69-75. labra; 76. postabdomen; 77. postabdominal claw;<sup>c</sup> 78.antennule.



Figs 79-92. Pleuroxus inermis Sars, 1896. All specimens from Frey sample 8026 (natural pond near Waroona, WA, 20 Nov. 1986). 79. instar-I male; 80. mature male; 81. headshield of parthenogenetic female; 82. headshield of ephippial female; 83. headshield of mature male; 84. rostrum of instar-II male; 85. rostrum of mature male; 86. antennule of mature male, showing a greatly elongate but smooth male seta (M); 87. antennule of instar-II male, showing substantial anlage of male seta (M'); 88. part of trunklimb I of instar-II male (CBS', anlage of copulatory brush seta; MS', anlage of male seta on IDL); 89. ODL and IDL of trunklimb I of mature male (MS, male seta; IDL3 not visible, nor was ODL2); 90. copulatory hook of mature male, showing three transverse ridges or crescents near tip; 91. postabdomen of mature male; 92. postabdomen of instar-II male (genital pore not discernible).

Victoria 14, 13 specimens, including several ephippial females; 9 are in clear medium and useable, the other 4 are varyingly obscured by bubbles.

2. Sars' liquid samples: a. F4137, Sydney, Australia, 14 parthenogenetic females; b. F4139, coll. Th. Whitelegge, 201 specimens, nearly all parthenogenetic females carrying eggs; c. F4140, coll. S. Ramsay, 46

parthenogenetic females.

Although a number of these samples have incomplete locality information and dates, slide F9672 and liquid sample F4139 are most significant, because they derive from material (mud?) collected by Th. Whitelegge near Sydney. Liquid sample F4140 was collected by Prof. S. Ramsay, who is the other



**Figs 93-106.** *Pleuroxus inermis* Sars, 1896. All specimens, except Fig.94, are parthenogenetic females from Frey sample 7961 (Wellington ferry crossing, River Murray, SA, 6 Nov. 1986). 93. parthenogenetic female; 94. ephippial female; 95-102. labra; 103 headshield of parthenogenetic female; 104, 105. postabdomens; 106. postabdominal claw.

person mentioned in Sars' description, and sample F4137 is from Sydney, possibly collected either by Ramsay or Whitelegge. Slides F9671 and F11731 from Victoria represent material acquired by Sars subsequent to the 1896 paper and are not mentioned in any of his later papers. It is likely that most of the specimens on slides and in the liquid samples were raised from dried mud.

3. Frey 7961 from the Wellington ferry crossing of the Murray River, SA, collected 6 Nov. 1986. 235



Figs 107-116. *Pleuroxus inermis* Sars, 1896. All specimens from Frey sample 7961 (Wellington ferry crossing, River Murray, SA, 6 Nov. 1986). 107. shell of parthenogenetic female; 108 antennule of parthenogenetic female; 109. antenna of parthenogenetic female, showing relatively small size of all three spines and relatively short length of basal endopod seta; 110. instar-I male; 111. instar-II male. 112. mature male; 113. rostrum of instar-II male; 114. rostrum of mature male; 115. postabdomen of instar-II male; 116. postabdomen of mature male (note much shortened postabdominal claw).

specimens, including ephippial females and all 3 instars of males, were removed from the estimated thousands of specimens in the sample.

4. Frey 8026 from a natural pond on Coronation Road from Waroona west to coast highway 1, WA, collected 20 Nov. 1986. This sample yielded a total of 221 specimens, including ephippial females and all three instars of males.

**Types.** LECTOTYPE – the top specimen, which is the middle one of five, on Sars' slide F9672 from Bourke Street, Waterloo, collected by Th. Whitelegge about 1892. A parthenogenetic female 0.59 mm long, well

preserved; PARALECTOTYPES – the other four parthenogenetic females on Sars' slide F9672, ranging in length from about 0.57 to 0.62 mm. The length could only be approximated, because the rostrum had been extended forward by coverglass pressure.

**Disposition of other specimens.** Slides of 1 parthenogenetic female from Sars' sample F4139, 1 parthenogenetic female, 1 ephippial female, 1 instar-II male, and 1 mature male from Frey sample 7961, and 1 parthenogenetic female from Frey sample 8026, all mounted separately in glycerine jelly, have been placed in the following museums. The numbers given are the



Figs 117-123. *Pleuroxus inermis* Sars, 1896. All specimens are from Frey sample 8026 (natural pond near Waroona, WA, 20 Nov. 1986). 117. parthenogenetic female; 118. ephippial female; 119. ephippium; 120. head end of dissected parthenogenetic female, showing antennule, antenna, labrum, mandible, and maxilla; 121, 122. postabdomen of parthenogenetic female (note that most denticles, at least distally, are single); 123. postabdominal claw.

catalogue or registration numbers.

	AM	NMNZ	BM(NH)	USNMNH
Sars F4139				
parthenogenetic	P39457	Cr. 6416	1989.603	242114
female				
Frey 7961				
parthenogenetic	P39458	Cr. 6417	1989.604	242115
female				
ephippial female	P39459	Cr. 6418	1989.605	242115
instar-II male	P39460	Cr. 6419	1989.606	242115
mature male	P39461	Cr. 6420	1989.607	242115
Frey 8026				
parthenogenetic	P39462	Cr. 6421	1989.608	242116
female				

All the remaining specimens from Frey samples 7961 and 8026 are in the Frey collection in Bloomington. The other specimens from Sars F4139 have been returned to the Zoology Museum in Oslo.

**Diagnosis.** Diagnosis and description are based mainly on sample 7961 because of the large number of specimens and the presence of all stages and instars. Any appreciable differences in morphology of specimens from Frey 8026 or Sars F4139 are mentioned. The specimens in Sars F4139 were difficult to dissect for details of head appendages and trunklimb morphology.



Figs 124-131. *Pleuroxus inermis* Sars, 1896. All specimens are from Frey sample 8026 (natural pond near Waroona, WA, 20 Nov. 1986). 124. instar-II male; 125. mature male; 126. rostrum of instar-II male; 127. rostrum of mature male; 128. postabdomen of instar-II male; 129. postabdomen of mature male; 130. antennule of instar-II male (M', anlage of male seta; AS, antennular seta); 131. antenna of mature male (M, male seta; AS, antennular seta).

Species highly arched dorsally. Posterior margin short, convex. No crest on head or shell. Shell without sculpturing except for about 6-10 short curved striae paralleling anterior margin. Usually no denticle at posterior-ventral angle in Western Australia population, nearly always present in Victoria population, variable in Sars' samples although nearly always present; small, easily overlooked. Well developed seta from basal segment of endopodite of antenna; seta from middle segment as long as distal setae; one of distal seta shorter than other 2; all distal setae of exopodite equally long; terminal spines very short, that of exopodite somewhat longer; spine from basal segment of exopodite very small, sometimes barely visible. Labral keel elongate, narrow, tip narrowly rounded. PP distance three and one half to four times IP distance. Roughly 89 ventral setae



**Figs 132-139.** *Pleuroxus inermis* Sars, 1896. All specimens are from Frey sample 7961 (Wellington ferry crossing, River Murray SA, 6 Nov. 1986). 132. ephippial female; 133. medial view of posterior-ventral angle with tooth and of fine setules along posterior margin, parthenogenetic female; 134. rostrum of parthenogenetic female; 135. claw of parthenogenetic female; 136. trunklimb I of parthenogenetic female (LS, lateral seta; ODL2, smaller and unfeathered seta of ODL; IDL3, short seta of IDL); 137, 138, postabdomen of mature male; 139. head end of instar-II male, showing labrum and antennule (M', anlage of male seta).

on shell, including those turned inward at anterior end. Rostrum ending in small rounded point. Postabdomen with preanal portion about equal in length to anal groove, and both considerably shorter than postanal portion; 12-13 marginal denticles, distal ones single, proximal ones with rows of setae proximally; distal half or less of preanal margin single. Postabdominal claw with 2 long, slender basal spines, larger one curved outward and longer than basal width of claw, smaller one slightly shorter. Ephippium with inner shell folded in dimpled fashion and containing some pigment; outer shell essentially without pigment. Rostrum of instar-II male short, broad, tipped with a rounded point; rostrum of instar-III male broadly truncate; antennule of instar-II male with well developed anlage of male seta, which is two thirds length of antennule in mature male but without setation on distal segment. Apparently 2 anlagen of setae at copulatory brush site in instar-II, but could not be resolved in instar-III specimens. Postabdomen of instar-II male very similar to female, of instar-III narrower and with longer postanal portion; claw of mature male shorter and stouter than of female, with 2 basal spines.

Parthenogenetic female. Shell and shape (Figs 48, 64, 78, 93, 107, 117, 133). Evenly curved dorsally, except for a flattening over headshield in Western Australia specimens. Posterior margin short, only one third total height, evenly convex. Ventral margin with weak bulge in front of middle, essentially straight behind this; provided with about 89 setae (range 82-97, n=40), all marginal except 8-10 most anterior setae, which are strongly submarginal and point posteriorly; setae on anterior half of shell arise from expanded bases. No sculpturing on shell except for about 6-10 short, curved striae anteriorly; these bend posteriorly and continue as 1-3 elongate striae closely paralleling ventral margin. Posterior-ventral angle with single minute denticle in Victoria sample, usually no tooth at all in Western Australia sample, and variable in Sars' samples. No keel on head or shell; body narrow, top rounded in frontal view.

*Head* (Figs 81, 103, 134). Although no keel present, difficult to get headshield to spread out because of extensive curvature from front to rear and from side to side. Rostrum short, tapers to a rounded point that almost seems to be stuck on separately. Somewhat constricted posteriorly and rounded. PP distance three and one half to four times IP distance (about 53-59  $\mu$ m in mature females); minor pores very small, less than 1 pore diameter apart. No sculpturing of any kind visible under phase optics.

Antennule (Figs 63, 78, 108, 120). Elongate, tapered distally, evenly curved. Short, rounded, posterior expansion at base. Nine aesthetascs, all arising from terminal portion, longest almost half length of antennule. Antennular seta arises two thirds from end, almost as long as longest aesthetasc.

Antenna (Figs 50, 109, 120, 147). Formula: 0(1)-0-3(1)/1-1-3(1). Terminal setae of exopodite all long, one of endopodite considerably shorter and thinner than

other 2. Setae from basal and middle segments of endopodite both well developed, that from middle segment as long as any terminal setae, that from basal segment half again as long as basal segment of middle or terminal setae. All 3 spines short, that of exopodite slightly longer than that of endopodite; spine from basal segment minute and sometimes not distinguishable.

*Labrum* (Figs 55-62, 69-75, 95-102, 120, 139). Elongate, narrow. Anterior margin convex, often with slight concavity near tip. Posterior margin long, irregularly concave. Posterior angle quite sharp, less than 90°. Tip of labrum usually narrow, rounded.

Trunklimb I (Figs 49, 67, 136). ODL with 2 setae, smallest of which is short, unfeathered; IDL with 3 setae. Two long IDL setae in typical fashion with row of setules on distal segment. Lateral seta well developed. Middle seta of middle group of corm setae much the longest.

*Trunklimbs II-V* (Fig.68). Setae in gnathobasic filter comb number 8, 8, 6 and 4, respectively. Feathered setae on exopodite 0, 7, 7 and 4, respectively. On trunklimb II, first 4 scraping spines shorter than number 5, all provided with row of very fine setules along distal segment.

Postabdomen (Figs 51-53, 76, 104, 105, 121-123, 135). Elongate; postanal margin weakly convex, tapering strongly to distal angle, rounded at tip. Preanal and anal segments about same length, each somewhat shorter than postanal portion. Postanal segment with about 12 straight, slender marginal denticles, distal ones all single, several proximal ones with row of spinules proximally. Anal groove with 4-6 successive rows of slender fringing spinules. Lateral surface with row of setular crescents along postanal portion, 2 rows along much of anal groove, 3 transverse rows at preanal angle and anterior to it. Ventral margin with 2 transverse crescents of fine setules. Distal half of preanal portion a single ridge with several weak diagonal furrows, proximal half more complex because of infolding and expansion. Abdominal setae somewhat longer than preanal segment.

*Postabdominal claw* (Figs 54, 77, 106, 123, 135). Long; both margins evenly curved. Concave margin provided with two sequential rows of fine setules. Two well developed but slender basal spines, distal one longer than basal width of claw, distinctly curved away from claw, proximal one straight, slightly shorter than width of claw.

**Ephippial female** (Figs 66, 82, 94, 118, 119, 132). Slightly more compressed from side to side than parthenogenetic female (cf. Figs 93 and 94, 117 and 118), hence headshield more elongate and attenuated posteriorly (Fig.82). Inner shell of ephippium lightly pigmented, outer shell unpigmented. On moulting, anterior-ventral portions of shell peel away from ephippium but remain attached posteriorly (Figs 66, 119). Inner shell pulls in around single ephippial egg, producing dimpled surface pattern dorsally (Fig.66). Other details of morphology as in parthenogenetic female.

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**Male.** Body much less high than in female (Figs 79, 80, 110-112, 124, 125, 140, 141). Rostrum of all 3 instars shorter than in female so that even in instar-I some aesthetascs extend beyond tip; rostrum of instar-II broad, short, tapered to small knob-like structure at tip (Figs 84, 113,126); rostrum of instar-III broadly truncate,

with rounded lateral angles (Figs 83, 85, 114, 127,144). Antennule of male broader than in female but with same rounded backward-projecting diverticulum at base; instar-II has well developed anlage of male seta (Figs 87, 130, 139); instar-III with this fully developed, but without any brush-like setation of distal segment (Figs



Figs 140-147. *Pleuroxus inermis* Sars, 1896. All specimens are from Frey sample 7961 (Wellington ferry crossing, River Murray, SA, 6 Nov. 1986). 140. instar-II male; 141. mature male; 142. trunklimb I of instar-II male (CBS', anlage of copulatory brush seta; MS', anlage of male seta); 143. trunklimb I of mature male (LS, lateral seta); 144. frontal view of mature male (note that the top is rounded, without a ridge or keel); 145. distal end of postabdomen and postabdominal claws of mature male; 146. head end of mature male, showing antennule, antenna, labrum, and part of trunklimb I (M, male seta; AS, antennular seta); 147. head end of parthenogenetic female, showing antennule (note posterior expansion at base) and antenna.

86, 131, 141, 146); antennular seta arises one third to one quarter from tip, closer to tip in instar-III; instar-III definitely has 12 aesthetascs as counted from their places of attachment as seen in terminal view. Trunklimb I shows typical changes in copulatory hook morphology from peg-like tooth in instar-I (Figs 79, 110) to well-developed U-shaped hook in instar-III (Figs 88-90, 142, 143), with the free limb very slender and with 3 rounded bumps (or crescents) near tip. Instar-II has 2 anlagen of setae at the site of the copulatory brush seta (Fig.88), the larger of which will become the copulatory brush seta in the next instar. Neither could be recognised with high-power phase in instar-III. Postabdomen of instar-I (Figs 79, 110) with postanal portion short, as in instar-I female, bordered by about 13 short slender denticles; ventral margin frequently irregular distally; genital pores not visible. Postabdomen of instar-II much the same as in female, except for waviness of ventral margin (Figs 92, 115, 128); genital pore slightly lateral and some distance from tip. Postabdomen of instar-III narrowed (Figs 91, 116, 129, 137, 138, 145), and postanal portion more elongate than in female; in Western Australia specimens, marginal denticles in proximal half are terminal member of transversely or diagonally oriented crescents (Figs 91, 129); South Australia specimens have more denticles distally, some doubled, and smaller crescents or rows proximally (Figs 116, 137, 138, 145); postabdominal claw shorter and stouter than in female, but still with 2 basal spines (Figs 91, 116, 138, 145).

**Length.** Western Australia (Frey 8026). Overall 0.30-0.57 mm (n=221). Females: instar-I 0.31-0.37 mm (n=88); instar-II 0.38-0.43 mm (n=26); mature 0.45-0.57 mm (n=49); smallest with eggs 0.45 mm; ephippial 0.47-0.55 (n=7). Males: Instar-I 0.30-0.36 mm (n=44); instar-II 0.38-0.40 mm (n=5); mature 0.40-0.43 mm (n=2).

South Australia (Frey 7961). Overall 0.33-0.63 (n=235). Females: instar-I 0.33-0.39 mm (n=54); instar-II 0.41-0.47 mm (n=40); mature 0.47-0.62 mm (n=95); smallest with eggs 0.47 mm; ephippial 0.54-0.63 mm (n=12). Males: Instar-I 0.34-0.37 mm (n=3); instar-II 0.41-0.46 mm (n=25); mature 0.45-0.47 (n=6).

New South Wales (Sars F4139). Overall 0.34-0.60 (n=199). Females: Instar-I 0.34-0.36 mm (n=3); instar-II 0.41-0.42 mm (n=6); mature 0.44-0.60 mm (n=190); smallest with eggs 0.44 mm.

**Comments.** These three populations are very similar but exhibit some differences, the significance of which is not yet understood. Thus, the various stages and instars in Frey 7961 are uniformly larger than the corresponding stages and instars of Frey 8026 (Fig.1). Frey 7961 has a slightly longer IP distance and a slightly shorter PP distance, yielding a PP/IP ratio averaging 3.3 instead of 3.8 as in Frey 8026 (Table 1). Frey 7961 has a single small tooth on the shell, which is only rarely absent, whereas Frey 8026 lacks a tooth in nearly all specimens, only occasionally having a single small tooth on one valve. In Sars F4139, 59% of 179 mature individuals had a single tooth on both valves, 20% a single tooth on one valve only, and 21% had no tooth. In addition, specimens from Sars F4139 have a longer secondary seta on the ODL than the other two populations. As already stated, such differences may have resulted from isolation of these populations from one another for some considerable period of time.

Of the various species of *Pleuroxus* seen in Australia, *P. inermis* seems the one most likely to be confused with *P. aduncus*. But although the females are vaguely similar, the mature males are not. This emphasises once again the fact that males are really needed to establish species and their limits and to decipher relationships between species.

The major differences in morphology between *Pleuroxus aduncus sensu stricto* from Denmark and *Pleuroxus inermis* from Australia are given in Table 3.

#### Pleuroxus hastirostris Sars

#### Figs 148-172

Pleuroxus hastirostris Sars, 1903: 635, figs 8, 8a-c.–Deevey, 1955: 302-303, figs 3-4,10-12,31.–Smirnov, 1971: 225, fig.207.

**Remarks.** Sars had only several parthenogenetic females from a collection from D'Urville Island, New Zealand, none of which are still extant. He considered that it resembled the Australian P. inermis, but that it lacked curved striae on the anterior part of the shell and it had a small but distinct tooth at the posterior-ventral angle. Deevey (1955) found abundant remains of P. hastirostris in sediments from Pyramid Valley on South Island, and Smirnov (1971) had material from a pond at Silverdale. Deevey's paper is non-taxonomic, although he makes some comments about the similarity of P. hastirostris to P. inermis and possibly to P. aduncus. His drawings of remains include an ephippium. Smirnov's (1971) description is based mainly on Sars (1903), and he copied Sars' three illustrations of the species. I have found the taxon in only one of the 157 samples I collected in New Zealand. In addition, V.M. Stout had specimens in her samples 12 and 84 from South Island. All available specimens are parthenogenetic females except for one male from the Frey sample. The species has not been reported from any other region and hence seems to be endemic to New Zealand.

**Material examined.** 1. Frey 8388 from Lake Waihola, south of Dunedin, 23 Mar. 1987, collected by D.G. Frey. Yielded 235 specimens, including one male.

2. Sample 12 from Rush Swamp off Pyramid, 29 Nov. 1964, collected by V.M. Stout. Yielded 5 parthenogenetic females. Stout has 4 samples from this locality, 2 each from 29 Nov. and 13 Dec. 1964.

3. Sample 84 from a farm pond between Oamaru and Timaru, 29 Aug. 1961, collected by V.M. Stout. Yielded 27 parthenogenetic females.

**Disposition of specimens.** One parthenogenetic female, mounted on a slide in glycerine jelly, has been deposited in each of the following museums: AM (P39463), NMNZ (Cr.6422), BM(NH) (1989.609), USNMNH (242117). All the other specimens from Frey 8388 plus the specimens in Stout's samples 12 and 84

are in the Frey collection in Bloomington.

**Diagnosis.** Body considerably longer than high; dorsal margin evenly rounded from rostrum to posteriordorsal angle, which is indistinct; posterior margin short, evenly but weakly convex; single small but distinct tooth



Figs 148-164. Pleuroxus hastirostris Sars, 1903. All specimens from Frey sample 8388 (Lake Waihola near Dunedin, NZ, 23 Mar. 1987). 148. instar-I female; 149. parthenogenetic female; 150. antenna of parthenogenetic female; 151. headshield of parthenogenetic female; 152. postabdomen of parthenogenetic female; 153. shell of parthenogenetic female; 154. posterior-ventral angle and posterior margin of shell of parthenogenetic female; 155-162. labra; 163. mature male; 164. postabdomen of mature male.

at posterior-ventral angle; ventral margin moderately bulged anterior to middle; about 8 or 9 short, faint striae paralleling anterior margin, no keel on head or shell. PP distance about 2.6 times IP distance in mature females; rostrum short and broad, ending in rounded point. Postabdomen tapers evenly from postanal angle, provided with about 8-10 long, slender denticles, nearly all of which have accessory setae associated with them; proximal denticles with long rows of long setae oriented obliquely to margin; single row of spinular crescents laterally; distalmost third of preanal portion single and with a couple of transverse ridges bearing rows of setae; anterior two thirds expanded laterally. Postabdominal claw with a row of setae along concave margin, a row of long thin setae along medial surface, and a sparse, ragged row of thin setae along convex margin; 2 basal



Figs 165-172. *Pleuroxus hastirostris* Sars, 1903. All specimens from Frey sample 8388 (Lake Waihola near Dunedin, NZ, 23 Mar. 1987). 165. parthenogenetic female; 166. postabdomen of parthenogenetic female; 167. rostrum of mature male; 168. inside view of posterior-ventral angle of shell and of setation along posterior margin of mature male; 169. dissected head end of mature male (M, male seta; AS, antennular seta); 170. trunklimb I of mature male (ODL2, smaller seta of ODL, showing slight feathering; MS, male seta); 171, 172. postabdomen and claws of mature male.

spines, distal one long and curved away from claw, proximal one straight and only about half as long. Male much less high than female; postabdomen narrower than in female, tapered distally from postanal angle, provided with about 9 rows of long setae oriented obliquely to margin; genital pore just above base of claw; postabdominal claw shorter than in female and with longer setae along concave margin; male seta on antennule long, tapered to sharp tip, without any feathering; antennular seta arises slightly distal of male seta; rostrum shortened, broadly rounded, with small tubercle medially, which is tucked underneath; tip of copulatory hook with 3 bumps near tip of concave margin; smaller seta on ODL well developed and weakly feathered terminally.

Parthenogenetic female. Shape and shell (Figs 148, 149, 153, 154, 165, 168). Dorsal margin highly and evenly rounded, with no concavity near posteriordorsal angle; no keel on head or shell; ventral margin weakly bulged ventrally anterior to middle, with continuous row of 78 (range 74-81, n=8) marginal setae. Anterior-ventral portion of shell with 8 or 9 short, faint striae, curving parallel to anterior margin, and continuing posteriorly as 1-3 straight striae close to and paralleling ventral margin (Fig.153), with very few cross connections; vague, short lines, like ridges, on shell, but no other markings except irregular polygonal ridges from contraction. Small but distinct and sharply pointed tooth just anterior to posterior-ventral angle, followed posteriorly by submarginal row of fine setae that continue to posterior-dorsal angle at somewhat greater distance from margin.

*Head* (Figs 149, 151). Rostrum short, broad, ending in rounded point; tip curving somewhat posteriorly, held away from body; IP distance 56 (range 54-59  $\mu$ m, n=6); PP/IP ratio 2.6. No keel behind headpores. Posterior margin rather broadly rounded. Eye oval, oriented transverse to margin; ocellus somewhat smaller; both almost touching margin.

Antennule. Elongate, rather slender, tapering distally. Nine aesthetascs, about one third to one half length of antennule. Antennular seta about one third from tip.

Antenna (Figs 150, 169). Formula: 0(1)-0-3(1)/1-1-3(1). Terminal setae of exopodite all long; one terminal seta from endopodite shorter, scarcely more than half length of other 2; seta from middle segment as long as terminal setae, that from basal segment well developed but only about half as long. Both terminal spines and spine from basal segment of exopodite very small.

*Labrum* (Figs 149, 155-162). Broad, short; irregularly convex anteriorly, weakly concave posteriorly; attenuated to broad, rounded tip; posterior angle moderately sharp, less than 90°.

*Trunklimbs I-V.* Few details observable; middle seta of middle group on limb I longest; gnathobasic filter setae 8, 6 and 4, respectively, on limbs III, IV and V; exopodite feathered setae 7,7 and 4 on limbs III, IV and V, respectively.

Postabdomen (Figs 152, 166). Preanal and anal portions about equal in length, both less than postanal

portion; latter tapers almost in straight line to rounded distal angle. Margin of preanal portion single in distal third with a couple of rounded transverse rolls; margin of proximal two thirds double from lateral expansion. 8-10 long, slender marginal denticles, each accompanied by up to 6 or even more long setae, those in middle clusters arranged somewhat obliquely. Single row of crescents of spinules parallels dorsal margin along lateral surface, with more complicated arrangement around preanal angle. Preanal angle reasonably distinct, postanal angle broadly rounded. Abdominal setae short, not reaching middle of anal groove when extended. Two crescents of fine spinules across ventral margin.

*Postabdominal claw* (Figs 152, 166). Long, slender, with hook-like bending at tip; continuous row of well-developed setae along concave margin to tip, another similar row along medial surface, third row of more slender seta along convex margin, giving ragged appearance. Two basal spines: distal one somewhat longer than basal width of claw, curved away from claw, proximal one only about half as long and straight.

Male (Figs 163, 164, 167, 169-172). The single specimen found was first drawn with the light microscope, then used for SEMs. Body elongate; shell anterior to ventral bulge slopes upward more strongly than in female and turns inward, thereby obscuring marginal setae. Rostrum short, broadly rounded, provided with small, bulb-like tip, which is recurved, partially obscured (Fig.169). Antennule broader than in female (Figs 163, 169). Male seta of antennule long, slender, tapering to fine point; arises about two fifths from tip (Fig.169); antennular seta arises slightly distal from here, very slender, tapering; seemingly only 9 aesthetascs, although these are always difficult to count. On trunklimb I, copulatory hook irregular at base, then tapers smoothly to narrow tip with 3 knobs on concave surface (Fig.170); smaller ODL seta well developed and feathered distally; male seta on IDL tapered gradually to sharp point, curved forward in direction of copulatory hook; lateral seta well developed; copulatory brush somewhat confused in SEM, and copulatory-brush seta not readily visible. Postabdomen narrower than in female (compare Figs 152 and 164, 166 and 171), tapers gradually from postanal angle to rounded tip distally; provided with about 9 short rows of long setae, oriented obliquely to dorsal margin (Fig.171), all about same size and hence difficult to designate any one as a denticle; lateral crescents of spinules, and 2 of small spinules across ventral edge, as in female; genital pores far distad, near base of claws (Fig.172). Postabdominal claws shorter than in female; setae along concave margin longer, and longer basal spine not so strongly curved, otherwise much the same.

**Length.** Lake Waihola females: overall 0.28-0.50 mm (n=234); instar-I 0.28-0.34 mm (n=62); instar-II 0.35-0.39 mm (n=112); smallest female with eggs 0.40 mm; male 0.39 (n=1). Stout sample 12: parthenogenetic females 0.46-0.52 mm (n=5). Stout sample 84:

parthenogenetic females 0.50-0.63 mm (n=27).

**Comments.** The considerable discrepancy in length of specimens between the Frey population and the two Stout populations suggested the possibility of two different species. However, all the Stout specimens agree closely in morphology with the Frey specimens, and, moreover, the shell drawn from Frey sample 8388 is much larger than that of any of the intact individuals collected, indicating that the maximum size of the taxon is considerably greater than suggested by the specimens in the sample.

#### Pleuroxus foveatus n.sp.

#### Figs 173-257

**Etymology.** From (L) *fovea*, a small pit, referring to the many small dimples covering the surface of the

shell.

**Comments.** The four populations representing this species are all from south-western Western Australia, two from the general region of Esperance and two from the Lake Muir region 400 km to the west. Hence, unlike a number of other species here reported that to now are known only from single localities, this taxon is quite widely distributed at least in Western Australia. Three of the four localities had conductivities between 3000 and 7000  $\mu$ S cm<sup>-1</sup>, indicating inland brackish water. Many of the waterbodies in this general region are endorheic and intermittent, and consequently would be expected to have variable salinity depending on their hydrologic phase. This particular species seems adapted to such conditions.

Three of the populations are very similar to one another, but the fourth is slightly different. A tabulation of some of the characteristics of each population is given below to indicate the extent of these differences.

		Length	1 et	Gnathobasic				IP length		Shall sataa		
Populati	ion	(mm)	eggs	II	III CO	IV	v	(um)	PP/IP	Mean	Range	
Shiel 8	57	0.38-0.71	0.51	8	9(8)	6	4	47	6.2	102	94-108	
Shiel 8	56	0.40-0.65	-	8	9	6	4	46	6.4	101	93-106	
Bayly 5	51	0.41-0.65	0.53	8	9	6	4	53	5.8	100	89-107	
Shiel 8	39	0.35-0.65	0.49	8	8(9)	6	4	55	4.7	102	100-113	

One of the distinctive characteristics of this taxon is nine setae in the gnathobasic filter comb of trunklimb III, but there is some variation. Thus, the type population had six limbs with nine setae and two with eight, and Shiel 839 had four with eight setae and two with nine. The latter population also has a slightly greater IP distance and a considerably smaller PP/IP ratio. The population available also seemed somewhat smaller, and first eggs occurred in smaller females (Fig.1). The PP distance is a problem, because it is measured as the chord distance in intact specimens. Hence, a greater curvature posterior to the pores could lead to a somewhat smaller ratio, although not to the seemingly significant reduction in ratio in Shiel 839. Other characteristics of this population, though, are quite concordant with the other three populations, so that (for the moment at least) it is considered to belong to the same taxon. Perhaps it represents the magnitude of differentiation that can occur among semi-isolated populations in these marginal waterbodies in Western Australia.

**Material examined.** *Type locality.* Flooded margin of Lake Muir, 50 km south-east of Manjimup, WA, collected 8 Oct. 1981 by R.J. Shiel, his accession number 857 (field number W.A. 67). The water at the time of sample collection was shallow, black and humic, and with a conductivity of 7000  $\mu$ S cm<sup>-1</sup>. The sample yielded 283 specimens, including abundant ephippial females and all three instars of males.

Other localities. (1) Small interconnecting channel between Lake Muir and Cowerup Swamp, located about 50 km south-east of Manjimup, WA, collected 8 Oct. 1981 by R.J. Shiel, his accession number 856 (field number W.A. 66). The water at this time was listed as black and peaty; conductivity 3500 µS cm<sup>-1</sup>. The sample yielded 16 individuals, including 5 males distributed among the three instars. (2) Shark Lake, 11.2 km north of Esperance, WA, collected 6 Oct. 1981 by R.J. Shiel, his accession number 839 (field number W.A. 48). The water was shallow, the bottom muddy, conductivity 3000 µS cm<sup>-1</sup>. The sample yielded 106 individuals, including 2 ephippial females and 3 mature males. Ostracods were the dominant organisms. (3) A roadside pond, 87 km west of Esperance on road to Ravensthorpe, WA, collected 27 June 1980 by I.A.E. Bayly, his sample 51. The sample yielded 35 specimens, all parthenogenetic females.

**Types.** HOLOTYPE – a parthenogenetic female 0.54 mm long, mounted on a slide in glycerine jelly, AM (P39464). ALLOTYPE – a mature male 0.47 mm long, mounted on a slide in glycerine jelly, AM (P39465). Special PARATYPES – 1 individual each of the following stages and instars, mounted separately on 2 slides in glycerine jelly, AM: an ephippial female 0.64 mm long (P39468), an instar-I male 0.39 mm long (P39467), and an instar-II male 0.45 mm long (P39466). PARATYPES – 1 slide each of a parthenogenetic female, an ephippial female, and a mature male, all mounted

in glycerine jelly, have been placed in several museums, as listed below. The numbers given are the catalogue or registration numbers of the specimens.

	AM	NZNM	BM(NH)	USNMNH
Shiel 857: PARAT	YPES			
parthenogenetic	— ·	Cr. 6423	1989.610	242118
female				
ephippial female	-	Cr. 6424	1989.612	212118
instar-II male	-	Cr. 6425	1989.613	242118
mature male	-	Cr. 6426	1989.611	242118
Shiel 839				
parthenogenetic	P39469	Cr. 6427	1989.614	242119
female				
ephippial female	P39470	_	_	_
mature male	P39471	_	_	-
Bayly 51				
parthenogenetic	P39472	Cr. 6428	1989.615	242120
female				

All the remaining paratypes and specimens from Shiel 856, 839, and Bayly 51 are in the Frey collection in Bloomington.

Diagnosis. Parthenogenetic female almost as high as long; median ridge on head behind pores and on shell; about 10 short curved striae anteriorly, roughly paralleling anterior margin, ventral tips uniting and continuing posteriorly as 1 or 2 longitudinal striae; small triangular tooth at posterior-ventral angle, followed along posterior margin by row of submarginal setules; entire surface of shell and of head behind pores dimpled; roughly 100 ventral setae, including about 10 at anterior end directed inward. Rostrum rather long, tapered to finely rounded, weakly offset tip; IP distance about 46-55 µm, PP distance 4.7-6.4 times IP distance. Antennule elongate, rather thin, tapered distally to small aesthetasc field, not surrounded by triangular points; 9 aesthetascs, one of which arises subterminally outside aesthetasc field; antennular seta arises about two fifths from end, about four fifths as long as antennule; backward projecting rounded extension at base. Antenna with 8 long swimming setae, one from basal segment of endopodite and one from each terminal group of three somewhat shorter than others. Labrum with elongate, narrow tip, convex anteriorly except for slight concavity near tip; posterior margin concave; posterior angle less than 90°, narrow. Trunklimb I with short second seta on ODL not feathered; middle seta of middle group of corm setae longest. Gnathobasic filter combs of trunklimbs II-V have 8, 9, 6 and 4 setae, respectively; exopodites of limbs III-V have 7, 7 and 4 feathered setae, respectively. Postabdomen with preanal and anal portions subequal, both shorter than postanal; about 13-15 long, slender marginal denticles, single distally but with 1 or more subdenticles or setae proximally; single row of spinular crescents along postanal and most of anal portions; several transverse rows in preanal region. Postabdominal claw weakly curved, concave border with 2 sequential rows of long setae; longer basal spine slender, curved, longer than basal width of claw; shorter basal spine about half as long. Body without pigmentation, only slight yellowish hyaline tinge. Ephippial female with 1 resting egg; lining of brood pouch darkly pigmented; shell in ephippial region more darkly hyalinised, with dimples and small tubercles; slough line proceeds to ventral margin, so that shell flaps easily lost on moulting. Good anlage of male seta on antennule in instar-II; postabdomens and claws of instar-I and instar-II males similar to females of these instars, except for genital pores and the irregular ventral margin in instar-II. Mature male has long, simple male seta on antennule, possibly only 9 aesthetascs; rostrum short, broadly rounded; postabdomen more elongate and more slender than in female, but marginal and lateral armament similar; genital pore near base of claw; postabdominal claw shorter, but otherwise resembles that of female.

Parthenogenetic female. Shape and shell (Figs 173, 174, 187, 199, 209-213, 242, 253). Body high, but not quite so high as long; uniformly curved from tip of rostrum to posterior-ventral angle, with only slight change in curvature at posterior-dorsal angle. Posterior margin weakly convex, with heavy line following closely submarginally. Ventral margin with mean of 102 setae (range 89-113, n=53), including about 10 setae anteriorly that bend inward instead of projecting away from body; setae of anterior third relatively unfeathered, those in posterior two thirds strongly feathered; each seta attached to a triangular swelling at base, producing weak serrate appearance. 10-15 short, curved striae at anterior end, roughly paralleling anterior margin, longest anteriorly, becoming progressively shorter posteriorly; shell striae fuse together ventrally and continue posteriorly as 1 or 2 striae closely paralleling ventral margin; some suggestions of meshes posteriorly (Figs 199, 212, 235, 237, 238), but not defined by any striae; entire shell and head posterior to pores covered by small dimples, but no other markings. Small triangular tooth at posterior-ventral angle (Figs 187, 242), occasionally absent or occasionally 2 teeth, followed by submarginal row of small setules along posterior margin to posteriordorsal angle. Body laterally compressed. Shell clear, without pigmentation.

*Head* (Figs 221-223, 239). Weak median ridge from behind pores to posterior-dorsal angle (Figs 240, 241). IP distance of mature females 46-55  $\mu$ m (n=24), PP distance (chord distance of whole specimens) 4.7-6.2 times IP; of males IP 42  $\mu$ m (n=4), PP distance 4.3 times IP. Minor pores about one pore diameter apart. Rostrum long, tapering to finely rounded tip that is weakly demarcated from rest of rostrum (Fig.239). Ocellus roughly quadrangular in shape; eye somewhat larger, ovoid, oriented with long axis perpendicular to dorsal margin; ocellus one third distance from eye to tip of rostrum. Head behind pores with fine dimples; anterior portion smooth.

Antennule (Figs 189, 222). Elongate, quite narrow, tapered distally; backward projecting rounded tubercle at base. Antennular seta about four fifths length of antennule, arising from prominent annulus about two fifths from tip. Nine aesthetascs, one of which seems to arise subterminally outside aesthetasc field; all

subequal in length. Aesthetasc field not surrounded by pyramidal points.

Antenna (Fig.223). Formula: 0(1)-0-3(1)/1-1-3(1). Eight long swimming setae; seta from basal segment of endopodite more than two thirds as long as terminal setae, and 1 terminal seta on each ramus somewhat

shorter than other 2. Terminal spines short, about one third as long as segments to which attached; spine from basal segment of exopodite very short, delicate.

Labrum (Figs 179-186, 214-219). Ventral tip elongate, narrow; anterior margin usually evenly convex except for slight concavity or waviness near tip; posterior



**Figs 173-187.** *Pleuroxus foveatus* n.sp. All specimens PARATYPES from Shiel sample 857 (margin of Lake Muir, WA, 8 Oct. 1981). 173. instar-I female; 174. parthenogenetic female; 175. ephippial female; 176. headshield of parthenogenetic female; 177, 178. postabdomen of parthenogenetic female; 179-186. labra; 187. posterior-ventral angle and posterior margin of shell of parthenogenetic female.

margin irregularly concave; posterior angle narrow and less than  $90^{\circ}$ .

*Trunklimb I* (Figs 188, 224, 225, 254). ODL with 2 setae, 1 very short, unfeathered (Fig.254). IDL with 3 setae, 1 of which is short, stout to the tip, and about

as long as basal segment of other 2, seemingly without any marginal setules; 2 long IDL setae with fringe of long, fine setules along distal segment (Fig.254). Middle seta of middle group of corm setae longest. Lateral seta from base of ODL-IDL ridge long, well developed,



Figs 188-198. *Pleuroxus foveatus* n.sp. All specimens PARATYPES from Shiel sample 857 (margin of Lake Muir, WA, 8 Oct. 1981). 188. trunklimb I of parthenogenetic female; 189. antennule of parthenogenetic female; 190. instar-I male; 191. mature male; 192. antennule of mature male (M, male seta, unfeathered; AS, antennular seta); 193. postabdomen of instar-I male; 194. postabdomen of instar-II male; 195, 196. postabdomen of mature male; 197. trunklimb I of instar-II male (CBS', anlage of copulatory brush seta; MS', anlage of male seta on IDL); 198. copulatory hook of mature male.



**Figs 199-208.** *Pleuroxus foveatus* n.sp. All specimens from Shiel sample 856 (interconnecting channel between Lake Muir and Cowerup Swamp, WA, 8 Oct. 1981). 199. shell of parthenogenetic female, showing distribution and size of a few dimples near posterior end; 200. postabdomen of parthenogenetic female; 201. mature male (note unequal lengths of aesthetascs and irregularity of ventral margin of postabdomen); 202. head end of instar-II male (M', anlage of male seta); 203. part of trunklimb I of instar-I male; 204. part of trunklimb I of instar-II male (CBS', anlage of copulatory brush seta; MS', anlage of male seta of IDL); 205. part of trunklimb I of mature male (CBS, copulatory brush seta; MS, male seta of IDL); 206. postabdomen of instar-II male; 208. postabdomen of mature male.

brush-like in distal two thirds.

*Trunklimbs II-V* (Figs 226, 227). Setae in gnathobasic filter comb 8, 9, 6 and 4 on limbs II-V, respectively; feathered exopodite setae 7, 7 and 4 on limbs III-V, respectively. On trunklimb II (Fig.226), margin between gnathobasic setae and scraping spines contains 2 or 3

setae close to gnathobase, often obscured by it, then a blunt broad seta or denticle, followed by an average of 7 (range 5-10, n=12) thick setae curved toward gnathobase, tips of proximal ones coarsely frayed; scraping spines 1-3 subequal in length, 4-6 subequal and longer, and 7-8 subequal and still longer, all provided



Figs 209-219. *Pleuroxus foveatus* n.sp. Specimens 210, 211, and 213-219 from Shiel sample 839 (Shark Lake near Esperance, WA, 6 Oct. 1981); specimens 209 and 212 from Bayly sample 51 (roadside pond west of Esperance, WA, 27 June 1980). 209, 210. parthenogenetic female; 211, 212. shell of parthenogenetic female; 213. posterior margin of shell and posterior-ventral angle of parthenogenetic female; 214-219. labra of parthenogenetic females.

with very fine setulation along distal segment.

*Postabdomen* (Figs 177, 178, 200, 230-233, 255). Anal groove equal to or slightly shorter than preanal portion, both considerably shorter than postanal portion. Preanal portion with 3 or 4 weak scallops in margin distally. Postanal portion with 13-15 long, slender marginal denticles, arising close together distally, further apart proximally; distal denticles single, proximal denticles with subdenticles and setae. Anal groove with about 5 sequential rows of fine setae that project well beyond margin. Lateral surface with row of crescentic clusters of spinules, generally 2 rows along anal groove,



**Figs 220-227.** *Pleuroxus foveatus* n.sp. All specimens from Shiel sample 839 (Shark Lake near Esperance, WA, 6 Oct. 1981). 220. ephippial female; 221. headshield of parthenogenetic female; 222, 223, rostrum, antennules, and antenna of parthenogenetic female (note small size of spines on antenna); 224, 225. trunklimb I of parthenogenetic female (LS, lateral seta; ODL2, shorter ODL seta, not feathered); 226. trunklimb II of parthenogenetic female; 227. gnathobasic portion of trunklimb III of parthenogenetic female.

up to 4 or 5 rows roughly perpendicular to preanal margin. Ventral margin not expanded basally; 2 crescents of fine spinules across ventral margin. Abdominal setae about one and one third times as long as preanal margin.

*Postabdominal claw* (Figs 177, 178, 200, 230, 255). Both dorsal and ventral margins weakly but evenly curved; concave margin with 2 sequential rows of long setae, those in distal row slightly longer. Both basal spines slender, evenly tapered and curved away from claw; longer one longer than basal width of claw, shorter one less than basal width. **Ephippial female** (Figs 175, 220, 235, 236, 251-253). Headshield much narrowed posteriorly, with weak triangular expansion opposite sloughline (Fig.251). Slough line evidenced by lines and irregular meshes, indicating where breakage will occur; extends to marginal patch of irregular meshes in front of posteriorventral angle, so that ephippium easily loses shell flaps completely but retains tooth and about 7-10 setae anterior to it. Sculpturing over ephippium a sequence of large dimples and small granules (Figs 236, 252). Pigmentation of broodpouch lining heavy, with darker hyalinisation of ephippial surface; sometimes difficult to



**Figs 228-234.** *Pleuroxus foveatus* n.sp. All specimens from Shiel sample 839 (Shark Lake near Esperance, WA, 6 Oct. 1981). 228. mature male (note the good development of both the male seta and the antennular seta); 229. part of trunklimb I of mature male; 230-232. postabdomen of parthenogenetic female; 233. postabdomen of instar-I female; 234. postabdomen of mature male.

see ephippial egg; rest of animal unpigmented. Heavy chitinous thickening along dorsal margin of shell, occasionally a notch or angle in contour where shell and head join on midline posteriorly (Figs 175, 220, 235).

**Male.** *Instar-I* (Figs 190, 193, 203, 206). Rostrum somewhat shorter than in female; aesthetascs reach tip. Trunklimb I with short finger-like anlage of copulatory hook. Postabdomen similar to that of instar-I female (compare Fig.233 with 193 and 206) with shortened postanal portion and a few rather coarse setae in groups along anal groove, all pointing distally; genital pore small, located some distance from end (Fig.193).

Instar-II (Figs 194, 197, 202, 204, 207, 237, 240, 246-

248). Rostrum still somewhat shorter (Fig.240); aesthetascs far exceed tip. Antennule with conspicuous anlage of male seta (Fig.202). Trunklimb I with J-shaped anlage of copulatory hook directed posteriorly, and with anlagen of male seta and copulatory brush seta. Postabdomen similar to instar-II female, except that ventral margin more irregular; genital pore has shifted more distally from its position in instar-I.

*Mature* (Figs 191, 192, 195, 196, 198, 201, 205, 208, 228, 234, 238, 241-245, 249, 250, 256, 257). Rostrum short, broadly rounded (Fig.241). Antennule with 2-segmented male seta, consisting of very long basal segment with little taper and apical segment without lateral setules (Figs 191, 192, 201, 243); seta about as



**Figs 235-241.** *Pleuroxus foveatus* n.sp. All specimens PARATYPES from Shiel sample 857 (margin of Lake Muir, WA, 8 Oct. 1981). 235. ephippial female; 236. patterning of shell of ephippial female, showing dimples; 237. instar-II male; 238. mature male; 239. rostrum of parthenogenetic female; 240. front view of instar-II male, showing especially ridge on top of shell and shape of rostrum; 241. similar view of mature male.

long as antennule, arising about midway; antennular seta almost as long, arising slightly more distally; seemingly only 9 aesthetascs, but difficult to count; antennule reaches tip of rostrum. Trunklimb I with well-developed male seta on IDL curving forward parallel to copulatory hook; copulatory brush seta largely hidden within copulatory brush; copulatory hook with very slender free branch (Fig.245), having 2 ridges on inside near



Figs 242-250. *Pleuroxus foveatus* n.sp. All specimens PARATYPES from Shiel sample 857 (margin of Lake Muir, WA, 8 Oct. 1981). 242. posterior-ventral angle and part of adjacent posterior margin of shell of mature male; 243. antennule and antenna of mature male; 244. tip of copulatory hook of mature male; 245. trunklimb I with copulatory hook of mature male; 246. trunklimb I of instar-II male (CBS', anlage of copulatory brush seta; MS', anlage of male seta on IDL; ODL2, smaller ODL seta); 247, 248. postabdomen and postabdominal claws of mature male; 249, 250. postabdomen and postabdominal claws of mature male.

tip, representing crescentic folds across hook (Fig. 244). Postabdomen elongate and narrowed (Figs 195, 196, 208, 234, 247), but with both anal angles distinct; has essentially same marginal and lateral armament as female; marginal denticles mostly single distally, multiple proximally, the latter arranged as crescents or rows arching away from margin; genital pore near tip and just slightly lateral of ventral midline. Postabdominal claw somewhat shorter than in female but otherwise with similar shape and armament. Anterior-ventral margin of shell straight in side view, coursing upward toward head (Figs 191, 201, 228); edges rolled inward, causing marginal setae to be indistinct.

Length. *Type series*. Females: overall 0.38-0.71 mm (n=204); instar-I 0.38-0.44 mm (n=89); instar-II 0.46-0.51 mm (n=32); smallest with eggs 0.51 mm; ephippial 0.58-0.71 mm (n=20). Males: Instar-I 0.37-0.43 mm (n=17), instar-II 0.41-0.48 mm (n=25); mature 0.46-0.54 mm (n=37). *Shiel* 856. Females: overall 0.40-0.65 (n=11); immature (mostly instar-I) 0.40-0.51 mm (n=9). Males: Instar-I 0.41 mm (n=1); instar-II 0.44-0.48 mm (n=2); mature 0.49-0.53 mm (n=2). *Bayly* 51. Females: overall 0.41-0.69 mm (n=35); instar-I 0.41-0.44 mm (n=4); instar-II 0.47-0.51 mm (n=10); smallest with eggs 0.53 mm. *Shiel* 839. Females: overall 0.35-0.65 mm (n=104); instar-II 0.35-0.39 mm (n=11); instar-II 0.40-0.65 mm



**Figs 251-257.** *Pleuroxus foveatus* n.sp. All specimens from Shiel sample 839 (Shark Lake near Esperance, WA, 6 Oct. 1981). 251. ephippial female; 252. surface sculpturing of shell of ephippial female, showing many small dimples; 253. head end of ephippial female; 254. ODL and IDL of trunklimb I of parthenogenetic female (note good size of ODL2, but without any, or only slight, feathering); 255. postabdomen of parthenogenetic female; 256. mature male; 257. postabdomen of mature male.
0.45 mm (n=14); smallest with eggs 0.49 mm. Mature males 0.43-0.47 mm (n=3).

#### Archepleuroxus Smirnov & Timms

### Archepleuroxus baylyi Smirnov & Timms

# Figs 258-314

Archepleuroxus baylyi Smirnov & Timms, 1983: 21, pl. 20a-i.

**Remarks.** The chief characteristic of this taxon, according to Smirnov & Timms (1983), is that it is polyembryonic, like *Saycia* and the various species of *Eurycercus*. They state that it is very similar in morphology to *Pleuroxus jugosus*, which is scarcely correct, and that it is quite similar to *Saycia*, which it can resemble only grossly. It is very similar to some of the other species of *Pleuroxus*-like forms, particularly those from Western Australia, but it differs so markedly from them, particularly in the structure of the postabdomen, that quite definitely it should be in a different genus.

Smirnov and Timms had the taxon from two localities in Victoria, seven in Tasmania, and one in Western Australia, the latter being the type locality. Only parthenogenetic females were present in these collections. Their description is incomplete and partially inaccurate. For example, the authors state that there are no head pores, that there is no spine arising from the basal segment of the antennal exopodite, and that the minimum length of females containing eggs is only 0.38 mm, compared with a minimum length of instar-I females of 0.33 mm. These length measurements suggest that the authors might well have had two different but similar appearing species present in their samples. These awkward discrepancies are corrected in the description in this paper.

## Justification for the Genus Archepleuroxus

Many of the morphological features of this taxon are shared by the species of *Pleuroxus* and related genera occurring in Australia: 1) the great height of the body of mature parthenogenetic and ephippial females; 2) the presence of a number of short, irregularly curved striae at the anterior end of the shell, and of suggestions of a vague pattern of reticulation posteriorly along the ventral margin; 3) the head pores quite close together and located some considerable distance (about five IP lengths) from the posterior margin; 4) the presence of eight long, two-jointed setae on the antenna; 5) a backward projecting, rounded basal expansion of the antennule; 6) the typically expanded labrum, prolonged into a rather narrow ventral tip; 7) the first trunklimb having the middle seta of the middle group by far the longest; 8) trunklimb II with scraping spines 1 to 3 subequal in length and considerably shorter than spine 4, all provided with many small setules along distal segment; 9) trunklimbs II to V having 8, 8, 6 and 4 gnathobasic filter setae, respectively, and 0, 7, 7 and 4 soft setae, respectively, on the exopodite; 10) ventral setae on shell are all marginal, except for the roughly ten most anterior setae, those in anterior region arising from triangular expansions at base, like teeth; 11) all three male instars being considerably lower in height than females; and 12) the ventral edge of the shell of the mature male anterior to the ventral bulge sloping upward strongly in a straight line and turned inward, thereby obscuring the marginal setae.

The chief differences from the other Pleuroxus-like species are in having more than two eggs in the larger parthenogenetic females and two resting eggs in ephippial females, and in the structure of the postabdomen. The latter is shorter and much broader than in any of the other species, it has the marginal denticles nearly all arranged as members of transverse or oblique rows of setae, and it has a complicated pattern of spinular crescents on the lateral surface and particularly along the anal groove and in the preanal region, where there are four chevron-like transverse folds, each with a row of strong setae. The postabdominal claws of male instars II and III are shorter than in the female and are quite distinctly sigmoid, or at least irregularly curved.

**Material examined.** 128 specimens recovered from Morton's sample 35 from a shallow temporary pond, 21 km north-west of Oatlands, Tasmania, collected 22 Aug. 1974. There was 6 mm of ice on the pond at this time. Smirnov and Timms had 30 samples from this expedition of Morton, which lasted 17 to 27 Aug. 1974, and although they mentioned *Archepleuroxus* being found under ice in a pool near Oatlands, the particular sample I have is not in their overall list nor in their list of positive localities. The sample examined had good numbers of all three instars of males and a few ephippial females, all of which have enabled a complete description of this taxon. Smirnov and Timms had no males.

**Disposition of specimens.** One slide each of a parthenogenetic female, an ephippial female, an instar-I male, and a mature male, all mounted individually in glycerine jelly, have been deposited in the following museums.

AM	NMNZ	BM(NH)	USNMNH
P39473	Cr. 6429	1989.616	242121
P39474	_	_	_
P39477	Cr. 6430	1989.619	242121
P39476	Cr. 6431	1989.618	_
P39475	Cr. 6432	1989.617	242121
	AM P39473 P39474 P39477 P39476 P39475	AM NMNZ P39473 Cr. 6429 P39474 – P39477 Cr. 6430 P39476 Cr. 6431 P39475 Cr. 6432	AM NMNZ BM(NH)   P39473 Cr. 6429 1989.616   P39474 - -   P39477 Cr. 6430 1989.619   P39476 Cr. 6431 1989.618   P39475 Cr. 6432 1989.617

All the remaining specimens are in the Frey collection in Bloomington.

Parthenogenetic female. Shape and shell (Figs

258, 263, 281, 294, 296). Large females almost as high as long, smaller females relatively more elongate. Dorsal margin highly convex and evenly curved from tip of rostrum to posterior-ventral angle; both posterior-dorsal



**Figs 258-272.** Archepleuroxus baylyi Smirnov & Timms, 1983. All specimens from Morton sample 35 (pond near Oatlands, Tas., 22 Aug. 1974). 258. parthenogenetic female (note the polyembryony); 259. shell of parthenogenetic female; 260. ephippial female, showing the two-egged condition; 261. headshield of parthenogenetic female; 262. rostrum of parthenogenetic female; 263. antennule of parthenogenetic female; 264. antenna of parthenogenetic female; 265-271. labra of parthenogenetic females; 272. postabdomen of parthenogenetic female.

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and posterior-ventral angles broadly rounded, with little change in curvature; ventral margin only weakly convex; usually no tooth on shell, but occasionally a very small tooth on one valve, and one specimen had four such teeth on one valve (Fig.296). Moderately flattened from side to side (Fig.294). No keel on head behind pores nor on shell. About 12 curved striae anteriorly on shell, becoming progressively shorter posteriorly (Fig.263). Row of fine marginal setae posterior to last ventral seta or tooth, continuing submarginally toward posterior-dorsal angle (Fig.296). Approximately 91 setae along ventral margin of shell, including about 10 arising from near anterior end projecting inward. Large females polyembryonic (Fig.258), with 22 embryos in holotype.

*Head* (Figs 261, 262, 294, 299). Headshield broad, unkeeled (Fig.261). Median pores in adult female about  $62 \mu m$  apart, located about 4.7 IP distances from posterior end. Rostrum relatively short, bluntly pointed at tip (Figs 262, 299); anterior part with a few indistinct



**Figs 273-280.** Archepleuroxus baylyi Smirnov & Timms, 1983. All specimens from Morton sample 35 (pond near Oatlands, Tas., 22 Aug. 1974). 273. trunklimb I of parthenogenetic female; 274. gnathobase and proximal four scraping spines of trunklimb II, parthenogenetic female; 275. trunklimb V of parthenogenetic female; 276. instar-II male; 277. instar-II male; 278. mature male; 279. antennule of instar-II male; 280. antennule of mature male (note much larger size of aesthetascs than for instar-II antennule; M, male seta; AS, antennular seta).

lines paralleling margin and also a few indistinct meshes. Articulation points for mandibles far removed from headshield-shell junction, as in all species in this paper. Aesthetasc field surrounded by obscure pyramidal tubercles.

Antennule (Figs 263, 282, 295). Elongate, slender,

evenly curved. Nine aesthetascs, about one third to two fifths length of antennule. Antennular seta arising about one third from distal end, longer than aesthetascs. Rounded protuberance at base, projecting posteriorly. Aesthetascs unequal in length, tips do not reach tip of rostrum.



Figs 281-290. Archepleuroxus baylyi Smirnov & Timms, 1983. All specimens from Morton sample 35 (pond near Oatlands, Tas., 22 Aug. 1974). 281. shell of mature male; 282. headshield of mature male; 283, 284. part of trunklimb I of instar-II male (CBS', anlage of copulatory brush seta; MS', anlage of male seta on IDL); 285. part of trunklimb I of mature male; 286, 287. postabdomen of instar-II male; 288, 289. postabdomen of mature male (note irregular claw); 290. postabdominal claw of mature male.

Antenna (Figs 264, 295). Formula: 0(1)-0-3(1)/1-1-3(1). Setae from basal and middle segments of endopodite both very long. Three long terminal setae on each branch, one somewhat shorter than other 2. Terminal spines short, less than half length of segment to which attached. Very small spine from basal segment of exopodite.

Labrum (Figs 265-271, 295, 314). Large, elongate;

anterior margin convex, usually smoothly but sometimes irregularly; tip narrowly rounded; posterior margin concave, usually with distinct angle one third to one half from tip; posterior angle narrow and less than 90°.

*Trunklimb I* (Fig.273). Two setae on ODL, smaller one with no distal spinules, only one about one third length of basal segment of longer seta; 3 IDL setae, 2



Figs 291-298. Archepleuroxus baylyi Smirnov & Timms, 1983. All specimens from Morton sample 35 (pond near Oatlands, Tas., 22 Aug. 1974). 291. parthenogenetic female; 292. ephippial female; 293. antennule of parthenogenetic female; 294. frontal view of parthenogenetic female; 295. labrum, antennules, and antenna of parthenogenetic female; 296. posterior-ventral angle and adjacent area of posterior margin of shell of parthenogenetic female (only specimen observed with more than one tooth at the angle); 297, 298. postabdomen of parthenogenetic female.

long with setose distal segment, other only about as long as proximal segments of longer setae, seems unarmed under phase optics. Lateral seta well developed. Middle seta of middle group of corm setae longest. All 3 accessory setae long, well developed.

Trunklimb II (Fig.274). Scraping spines 1-3 subequal in length, considerably shorter than spine 4, all with very fine and almost uncountable spinules along margin of distal segment. Three gnathobasic setae and one much smaller and blunter seta on margin toward scraping spines, the latter preceded by 3 straight setae and followed by about 15 stout curved setae, of which the first several have setules near their tips. Eight gnathobasic filter setae.

Trunklimbs III-V. Only limb V (Fig.275) clear in dissection. Exopodite soft setae numbered 7, 7 and 4, and the gnathobasic filter setae 8, 6 and 4, respectively. *Postabdomen* (Figs 272, 297, 298). Relatively short,

broad. Anal groove shorter than preanal and postanal parts, which are subequal. Preanal portion with series of 3-4 scallops near preanal angle, representing rounded ridges across margin and angled distally on either side, like chevrons. Postanal portion with about 12 positions for denticles, each position except a few of most distal ones occupied by short row of denticles or setae arranged transverse to margin. Lateral surface with irregular row of scallops of setae, with 3-4 rows along anal groove and in preanal region. Two scallops of short setae across ventral margin. Anal groove bordered by about 5 distinct groupings of setae arranged sequentially. Abdominal setae short, barely reaching anal groove when extended.

*Postabdominal claw* (Figs 272, 297). Stout, evenly curved, with fine setules along entire concave margin. Two basal spines, longer one slender, curved, about as long as basal width of claw; shorter one very slender,



Figs 299-305. Archepleuroxus baylyi Smirnov & Timms, 1983. All specimens from Morton sample 35 (pond near Oatlands, Tas., 22 Aug. 1974). 299. Rostrum of parthenogenetic female; 300. rostrum of instar-I male; 301. rostrum of instar-II male; 302. rostrum of mature male; 303. surface patterning of shell of ephippial female; 304. instar-I male; 305. mature male.

straight, only about half as long.

**Ephippial female** (Figs 260, 292, 303). Two ephippial eggs. Ephippial portion of shell heavily pigmented. Headshield narrower posteriorly than in

parthenogenetic female to meet contracted shell, with which it forms a distinct angle in outline (Fig.260); distinct triangular expansion at beginning of slough line. Dorsal edge thickly chitinised. Surface of ephippium finely dimpled (Fig.303), but no other sculpturing.



**Figs 306-314.** Archepleuroxus baylyi Smirnov & Timms, 1983. All specimens from Morton sample 35 (pond near Oatlands, Tas., 22 Aug. 1974). 306. trunklimb I of instar-I male (CH', anlage of copulatory hook); 307. trunklimb I of instar-II male; 308. trunklimb I of mature male; 309, 310. postabdomen of instar-I male; 311-313. postabdomen of mature male; 314. rostrum, antennules, antenna, and labrum of mature male (M, male seta).

Other details of morphology same as in parthenogenetic female.

Male. Copulatory hook develops gradually (Figs 276-278, 283-285, 306-309). Anlagen of copulatory brush seta (actually 2 anlagen here), of male IDL seta on trunklimb I (Figs 283, 284), and of male seta on antennule (Figs 277, 239) appear in instar-II. Rostrum shorter than in female, pointed in instar-I (Fig.300); rounded and progressively shorter in instars II and III (Figs 282, 301, 302), first with only the aesthetascs and then antennule also projecting beyond tip of rostrum. Postabdomen similar in shape and armament to that of female, although less broad (Figs 286-289, 309-313); genital pore moves progressively distad to its definitive position in instar-III slightly lateral near base of postabdominal claw (Figs 289, 312). Postabdominal claw of instars II and III shorter than in female and somewhat sigmoid (Figs 286, 287, 311, 313). In shape, all three instars more elongate (less high) than corresponding instars of females (Figs 276-278, 304, 305). PP distance only twice IP distance (or even a little less in instar-I), contrasting with 4.7 times IP distance in mature parthenogenetic and ephippial females. Postabdomen of all 3 instars provided throughout postanal region with transverse groups of stoutly chitinised setae (Figs 286, 287, 289, 309-313). Mature male seems to have only 9 aesthetascs, and certainly fewer than 12, some of which are about two thirds length of antennule, and all much longer and thicker than in instar-II male (compare Figs 279 and 280) or in females.

**Length.** Females: 0.39-0.95 mm (n=128); instar-I 0.39-0.44 mm (n=14); instar-II 0.49-0.56 mm (n=31); smallest parthenogenetic female with eggs 0.62 (n=27); ephippial females 0.67-0.78 mm (n=3). Males: instar-I 0.39-0.43 mm (n=14); instar-II 0.44-0.50 mm (n=9); instar-III (= mature) 0.51-0.56 mm (n=17).

#### Plurispina n.gen.

**Type species.** *Plurispina chauliodus* n.sp. by original designation.

**Diagnosis.** The following characters are shared by the two species described here: 1) a comparatively large number of setae in the gnathobasic filter combs of trunklimbs II-V - 10, 10, 7 and 5, respectively, instead of the more common 8, 8, 6 and 4; 2) shell and head covered by small rounded tubercles, which in the case of *P. multituberculata* are so densely placed that they create a general opacity; 3) radial ridges on shell and raised meshes on dorsal part of shell and adjacent headshield; 4) a strong keel beginning immediately behind posterior headpore, continuing to posterior-dorsal angle of shell, and 5) a strong flaring out proximally of the ventral margin of the postabdomen. Parthenogenetic females of both taxa are high in

relation to length, with dorsal margin highly arched and ventral margin much less so. The posterior-dorsal corner of the shell is essentially absent as any perceptible change in curvature here, and the posterior-ventral angle is likewise almost eliminated. Here in both species there is a very small rounded or triangular tooth, with number per valve varying from none to two. Ventral setae, including inwardly directed anterior setae, average 107 in *P. chauliodus* and 122 in *P. multituberculata*; those anterior to the midventral bulge have expanded bases that are strongly chitinised and superficially resemble the teeth of a saw.

**Etymology.** From (L) *plus, pluris* more, and (L) *spina* spine (feminine gender), referring to the larger number of setae in the gnathobasic filter combs of trunklimbs II-V.

**Remarks.** Other than number of setae, the morphology of the two species is rather divergent, so that not too much can be said about common characters. Unfortunately, no males of *Plurispina multituberculata* are available, and hence there is no way of knowing if the brush-like nature of the male seta on the antennule in *Plurispina chauliodus*, the general shape and armament of the male postabdomen, and the presence of two prominent submarginal denticles on the rostrum of the male are unique for this species or characteristic of the genus.

#### Plurispina chauliodus n.sp.

Figs 315-375

Pleuroxus jugosus.-Smirnov & Timms, 1983: 22-24, figs 21, 22 (not Chydorus jugosus Henry, 1922).

**Etymology.** From (Gr) *chauliodus* with projecting teeth, or tusked (common gender), referring to two prominent submarginal denticles on rostrum of mature male.

Remarks. Smirnov & Timms (1983) used specimens from Bayly's sample 58 (their sample 420) to expand the morphological understanding of Henry's taxon. They included drawings of a female and its headshield, postabdomen and head pores, and of a mature male with its postabdomen and tip of the rostrum. They pointed out that the shell and head are finely punctate (= tuberculate) and that the rostrum of the male is provided with two spines, the latter being a character ...not described for any other cladoceran..." Unfortunately, all these new morphological details do not apply to Pleuroxus jugosus at all, as the two taxa are even in different genera. The description of P. jugosus, incomplete though it is without mature females, males, and ephippial females, will be as given later in this paper.

**Material examined.** *Type locality.* Granite pool in Muirillup Rock near Northcliffe, WA (Bayly, 1982: fig.4), collected by I.A.E. Bayly: sample 31 on 4 June, sample 58 on 18 June (= Smirnov & Timms sample 420), and sample 84 on 2 July, all in 1977. Numbered N11 in Bayly's system, this pool measured 2.8 x 1.4 m and

was 4 cm deep. Its pH varied from 5.8 to 6.4, and its conductivity at  $18^{\circ}$ C was 61-70  $\mu$ S cm<sup>-1</sup>.

**Types.** 167 specimens from samples 31 (83 individuals), 58 (49), and 84 (25), plus various exoskeletal components. Specimens from the three



**Figs 315-327.** *Plurispina chauliodus* n.sp. All specimens PARATYPES from Bayly samples 31, 58, and 84 (granite pool on Muirillup Rock near Northcliffe, WA, 4 and 18 June and 2 July 1977, respectively). 318 and 319 are from sample 31; 315 and 321-327 are from sample 58; and 316, 317, and 320 are from sample 84. 315. parthenogenetic female; 316. ephippial female; 317. ephippium; 318-321. headshield of parthenogenetic females with antennules included in 321; 322-327. labra of parthenogenetic females.

samples agree exactly in their morphology and size relationships. Drawings from all three are included in the description. Registration numbers are given in parentheses below. HOLOTYPE - a mature

parthenogenetic female 0.70 mm long, mounted on a slide in glycerine jelly, AM (P39478). ALLOTYPE – a mature male 0.62 mm long, mounted on a slide in glycerine jelly, AM (P39479). Special PARATYPE – an



**Figs 328-336.** *Plurispina chauliodus* n.sp. All specimens PARATYPES from Bayly samples 31, 58, and 84 (granite pool on Muirillup Rock near Northcliffe, WA, 4 and 18 June and 2 July 1977, respectively). 328 is from sample 31, 329 from sample 84, and all others are from sample 58. 328. rostrum and associated head appendages of parthenogenetic female; 329. antenna of mature male; 330, 331. trunklimb I of parthenogenetic female (330 is a medial view without the ODL and IDL; 331 is only of the ODL and IDL; ODL2, shorter ODL seta, feathered); 332. gnathobase and three adjacent scraping spines of trunklimb II of parthenogenetic female; 333.gnathobase of trunklimb III of parthenogenetic female; 334. gnathobase of trunklimb V of parthenogenetic female; 335, 336. postabdomen of parthenogenetic female.

ephippial female 0.89 mm long, mounted on a slide in glycerine jelly, AM (P39480). PARATYPES -1 slide each in glycerine jelly of a mature parthenogenetic female, a mature male, and an ephippial female have been deposited in each of the following

museums.

	NMNZ	BM(NH)	USNMNH
parthenogenetic female	Cr. 6433	1989.620	242122
mature male	Cr. 6434	1989.621	242122
ephippial female	Cr. 6435	1989.622	242122



**Figs 337-346.** *Plurispina chauliodus* n.sp. All specimens PARATYPES from Bayly samples 58 and 84 (granite pool on Muirillup Rock near Northcliffe, WA, 18 June and 2 July 1977, respectively). 337 and 344 are from sample 58, the rest from sample 84. 337. instar-II male; 388. mature male; 339, antennule of mature male; 340, 341. tip of labrum of mature male, showing two submarginal tusk-like denticles; 342. ODL and IDL of trunklimb I of mature male; 343. exopodite of trunklimb III of mature male; 344. postabdomen of instar-II male (genital pore not visible); 345, 346. postabdomen of mature male.

**Diagnosis.** Body almost as high as long, evenly curved dorsally, with posterior-dorsal angle virtually lacking. Shell with series of interrupted curved striae anteriorly, and with straight cross connections formed by rows of tubercles; radiating ridges along ventral and dorsal margins; about 107 ventral setae, ending posteriorly in a small, broad-based triangular tooth, followed by a marginal-submarginal row of short but regular setules extending to posterior-dorsal angle; tip of rostrum weakly bifid. Short seta on ODL well developed and brush-like. Ten, 10, 7 and 5 setae in gnathobasic filter combs of trunklimbs II to V, respectively, and the more typical 7, 7 and 4 feathered

exopodite setae on limbs III-V. Postabdomen with preanal portion much shorter than anal or postanal portions, provided distally with 4 or 5 distinct rounded scallops resulting from rounded chevron-like folds across dorsal margin; 12-15 denticles or denticle positions, mostly multiple, and all members long and slender; abdominal setae short, not extending far into anal groove region when depressed. Postabdominal claw with long and strong setae along dorsal margin; basal spines thin and relatively short. Ephippial female with very dark pigmentation that obscures morphological details; single resting egg. Male II with more slender postabdomen than female; genital pore near base of



**Figs 347-353.** *Plurispina chauliodus* n.sp. All specimens PARATYPES from Bayly sample 84 (granite pool on Muirillup Rock near Northcliffe, WA, 2 July 1977). 347. parthenogenetic female; 348. fine tubercles on shell of parthenogenetic female; 349. top view of parthenogenetic female, showing shape of headshield and marked keel beginning just behind posterior headpore; 350. ephippial female; 351. front view of ephippial female, showing rostrum and sharp keel beginning just behind posterior headpore; 352. ephippium; 353. surface patterning of dimples and tubercles in ephippial portion of shell.

claw; well developed male seta anlage on antennule. Male III has shortened rounded rostrum with 2 stout submarginal denticles; male seta on antennule long, distal segment brush-like; postabdomen slender, tapered to base of claw, provided with about same number of denticle positions as in female but all denticles stout and well chitinised; postabdominal claw shorter and stouter than in female, strongly curved, provided with long setae along concave margin. Colour dark.

Parthenogenetic female. Shape and shell (Figs 315,

347-349, 356, 492). Body very high, but still somewhat longer than high; dorsal margin evenly curved from tip of rostrum to posterior-ventral angle, with only small convexities over eye and ocellus (Fig.315); posterior margin short, weakly but evenly convex; ventral margin convex, with maximum curvature (= ventral bulge) just anterior to middle. Shell covered nearly everywhere by radiating ridges, about 7-11 of those in front associated with short striae paralleling anterior margin of shell (Fig.317), those behind associated with rows of tubercles, which also produce cross connections; row



Figs 354-360. Plurispina chauliodus n.sp. All specimens PARATYPES from Bayly sample 84 (granite pool on Muirillup Rock near Northcliffe, WA, 2 July 1977). 354. head end of parthenogenetic female, showing rostrum, labrum, antennule, and antenna (note long terminal spines on antenna); 355. junction of ecdysial line and slough line on shell of ephippial female; 356. posterior-ventral angle with small shell tooth and with adjacent setulated portion of posterior margin, parthenogenetic female; 357. headpores and keel of parthenogenetic female (MP, minor pores); 358. antennules of parthenogenetic female, showing pointed triangles surrounding aesthetasc field; 359. postabdomen of parthenogenetic female; 360. postabdominal claw of parthenogenetic female (note straight basal spines and long setae along concave margin).

of 107 setae (range 100-113, n=17) along ventral edge of shell, including those turned inward at anterior end, terminating at a broad-based triangular denticle at posterior-ventral angle, which is followed by a marginalsubmarginal row of closely spaced setae that continue toward posterior-dorsal angle (Fig.356). Entire surface of shell and head, except for marginal borders, covered with rather densely spaced, rounded tubercles (Figs 348, 357). Strong keel on head beginning immediately behind posterior pore (Figs 349, 357), continuing to posterior-dorsal angle. Colour dark brownish, and hence difficult to discern details.

*Head* (Figs 318-321, 328, 349, 357). Rostrum short and broad (Fig.320), weakly bifid at tip (Fig.321); suggestions of submarginal line and meshes from the lining up of denticles into rows. IP distance roughly 42  $\mu$ m; PP distance 7.6 times IP distance or even more; strong keel behind posterior pore, sometimes produces change in curvature as seen from side. Minor pores about two major pore diameters apart (Fig.357).

Antennule (Figs 321, 358). Long and narrow, tapering toward distal end, which is provided with series of triangular tubercles around aesthetasc field; rounded evagination directed posteriorly at base; 9 aesthetascs, all terminal, about one third length of antennule; antennular seta about twice as long, arising about one third from tip of antennule; tips of aesthetascs much shorter than tip of rostrum.

Antenna (Figs 328, 329, 354, 367). Formula: 0(1)-0-3(1)/1-1-3(1). Eight long swimming setae; one of 3 terminal setae on endopodite considerably shorter than other 2, about same length as long seta arising from basal segment of endopodite. Both terminal spines long, about as long as segments from which they arise, and spine



Figs 361-366. Plurispina chauliodus n.sp. All specimens PARATYPES from Bayly sample 84 (granite pool on Muirillup Rock near Northcliffe, WA, 2 July 1977). 361. mature male; 362. anterior margin of shell of mature male, showing dense mass of long fine setae occurring here; 363. surface of shell of mature male, showing radiating ridges and fine tubercles; 364. inside view of posterior-ventral angle and posterior margin of shell of mature male; 365. postabdominal claws of instar-II male; 366. postabdominal claws of mature male.

from basal segment of exopodite well developed. Transverse rows and crescents of fine spinules on 3 segments of both rami and on basal segment.

Labrum (Figs 322-327, 354). Broad, and with rather

short tip, which is usually quite broadly rounded; anterior margin evenly curved; posterior margin mostly straight, sometimes weakly convex; posterior angle often quite narrow, less than 90°.



Figs 367-375. Plurispina chauliodus n.sp. All specimens PARATYPES from Bayly sample 84 (granite pool on Muirillup Rock near Northcliffe, WA, 2 July 1977). 367. rostrum of instar-II male; 368-369. rostrum of mature male, showing the two submarginal tusk-like denticles (TD) and the highly feathered male seta on the antennule (M); 370-372. postabdomen and claws of mature male; 373. trunklimb I of mature male, showing slender copulatory hook (ODL2, short seta on ODL, feathered; CBS, copulatory brush seta); 374. attenuated tip of copulatory hook of mature male; 375. antennules of instar-II male (M', anlage of male seta; AS, antennular seta).

Trunklimb I (Figs 330, 331). Small seta on ODL, almost half as long as basal segment of longer ODL seta; with distal segment brush-like from short setules; 3 setae on IDL, shortest of which barely reaches tip of basal segment of other 2. Middle seta of middle group of corm setae the longest.

*Trunklimb II* (Fig.332). Ten setae in gnathobasic filter comb; 3 gnathobasic setae, followed toward scraping spines by 3 straight slender setae, then a welldeveloped thickened seta or denticle, and this by about 10 long, thick setae curving distally toward gnathobase. Scraping spines 7 and 8 considerably longer than expected from mere increase in size sequentially; other 6 scraping spines with very fine setules along outer segment.

*Trunklimbs III-V* (Figs 333, 334, 343). Setae in gnathobasic filter comb number 10, 7 and 5 (4 in male), respectively, and 7, 7 and 4 feathered setae on the exopodite, respectively. On trunklimb III, the 2 'hard' setae farthest from gnathobase are heavily chitinised and almost spine-like (Fig.333), projecting ventrally in intact animal in opposition to trunklimb I, especially; longest feathered seta on exopodite only slightly longer than next longest (Fig.343).

Postabdomen (Figs 335, 336, 359, 493). Anal groove about as long as postanal portion; preanal portion much shorter, with a series of 4-6 distinct rounded scallops in margin distally. About 12-15 marginal denticle positions; denticles long and slender, seldom single except occasionally distally, organised into a series of clusters or rows proximally, which are oriented parallel to margin. Preanal and postanal angles, especially the latter, very weakly developed; anal groove protected by series of about 7 groups of slender setae projecting beyond margin; distalmost member of each group stouter (Fig.335). Postanal portion with single row of curved crescents laterally, 2 rows along anal groove, and essentially none in preanal region. Two big crescents of fine spines across ventral margin. Abdominal setae short, reaching only to about proximal third of anal groove when extended. Ventral margin flares outward basally.

*Postabdominal claw* (Figs 335, 336, 359, 360). Stout; rather blunt toward tip; concave margin curved about one third from base, then almost straight to tip. Concave margin with 2 series of long and conspicuous spinules, extending to tip, those in distal series longer. Two short basal spines: longer one about as long as basal width of claw, smaller one very slender and only about half as long.

**Ephippial female** (Figs 316, 317, 350-353, 355). Shape similar to that of parthenogenetic female (compare Figs 315 and 316, 347 and 350). Headshield much narrowed posteriorly, providing thereby more shell for the ephippium. Slough line very distinct, particularly ventrally (Figs 350, 352); toward ecdysial line bordered by small angular meshes (Fig.355), which obviously help in separation of anterior and ventral strip from ephippium on molting; these remain broadly attached at posterior end (Fig.352), forming 2 outward curving hooks or flaps. Inner lining of shell in ephippial region very darkly pigmented (Figs 316, 317), thereby obscuring any details underneath. Single ephippial egg. Surface of ephippium with closely packed tubercles, and even more closely packed in dimples that cover surface irregularly (Fig.353).

**Males.** *Instar-II* (Figs 337, 344, 364, 365, 367, 375). Body less high than in parthenogenetic female but otherwise similar in morphology (Fig.337). Postabdomen more slender than in female, but with same armament of marginal denticles and same clusters of setules along anal groove (Fig.344). Clusters of denticles oriented along length of postabdomen, not transversely diagonal to it. Lateral clusters of spinules in only specimen available visible in postanal portion but not elsewhere, seemingly similar to female; genital pore near base of claw but less close to it than in instar-III. Details of trunklimb I not visible. Rostrum shorter than in female, but with a similar weak evagination. Antennule with well developed anlage of male seta.

Instar-III (Figs 329, 338-343, 345, 346, 361-363, 366, 368-374). Body still lower relatively than in instar-II (Figs 338, 361). Portion of ventral margin anterior to midventral bulge sloping upward, straight, and with margin rolled inward, thereby obscuring ventral setae (Figs 338, 361); setae here have long, slender branches, creating a fuzzy appearance along this margin (Fig.362). Headshield shorter than in female, broad and roundly truncate at tip, provided with two stout denticles that arise submarginally and project beyond margin (Figs 340, 341, 368, 369). (Smirnov noted these and illustrated them in his drawings supposedly of Pleuroxus jugosus.) Antennules broader than in female, provided with very long male seta that is strongly brush-like distally (Figs 339, 369); antennular seta not quite so long, arising about one third from tip; seemingly only 9 aesthetascs. Trunklimb I with characteristic 3 IDL setae, plus large male seta (Fig.342); copulatory hook long and slender, with 3 crescentic ridges near tip (Figs 373-374). Postabdomen slender, and with preanal and postanal angles even less distinct than in female, but with relative lengths of the 3 zones about same as in female and with similar deployment of setular crescents and rows laterally, although with greater irregularity in placement (Figs 345, 346, 370-372); genital pore very near base of claw (Fig.372); about 13 denticles or denticle positions, mostly multiple and all heavily chitinised, those in proximal groups arranged obliquely; ventral margin flares outward basally (Figs 345, 346). Abdominal setae short, as in female. Distal tip of postabdomen narrowed and without claw stump or peduncle present in female. Postabdominal claw shorter and stouter than in female, strongly curved and provided with long setae along entire concave margin (Figs 345, 346, 366, 372); larger basal spine less than basal width of claw in length, smaller spine still smaller and not always easily visible.

**Length.** Females: overall 0.49-0.90 mm (n=137); instar-I 0.49-0.58 mm (n=25); instar-II 0.60-0.68 (n=54);

first embryos at 0.68 mm; ephippial 0.77-0.90 (n=13). Males: instar-II 0.63-0.65 (n=2); instar-III (= mature) 0.63-0.70 mm (n=15).

## Plurispina multituberculata n.sp.

## Figs 376-402

**Etymology.** From (L) *multus* many, and (L) *tuberculum* tubercle, referring to the densely packed tubercles on the shell and head.

Remarks. Although only parthenogenetic females are available for this taxon, thereby precluding a complete description of its morphology, it seems to belong to the same genus as Plurispina chauliodus, with 10, 10, 7 and 5 setae in the gnathobasic filter combs of trunklimbs II-V, respectively, and in the general pattern of its morphology. The following characters differentiate it from its congener: 1) the shell is completely covered with radiating ridges and large, densely packed tubercles; 2) the tip of the rostrum is bead-like, rather than weakly bifid; 3) the labrum is elongate, rather than short and broad; 4) the smaller seta on the ODL is not strongly brush-like, possibly weakly so; 5) the anal groove is relatively much shorter, only about as long as the preanal portion instead of as long as the postanal portion; and 6) the rounded scallops in the distal portion of the preanal region are fewer and less well developed. Males and ephippial females are needed to define this taxon precisely. Because the type locality of this taxon is in the same general region of extreme south-western Australia as that for Plurispina chauliodus, and because the two species are from essentially the same kind of small pools in granite bedrock, it seems likely that there may well be a whole suite of related species of this genus or of other genera that could be discovered with intensive investigation. Smirnov & Timms (1983) have this sample listed as number 423 in their treatment of Pleuroxus jugosus.

**Material examined.** *Type locality.* Pool in granite, Dutarning Range, south of Perth, WA (Bayly, 1982: fig. 6), collected 24 June 1977 by I.A.E. Bayly, his field number 66.

**Types.** All 48 specimens plus exuviae from Bayly's sample 66 from the type locality. HOLOTYPE – a mature parthenogenetic female 0.81 mm long, mounted on a slide in glycerine jelly, AM (P39481). PARATYPES – a mature parthenogenetic female and an instar-I female mounted in glycerine jelly under the same coverslip have been deposited in each of the following museums: NMNZ (Cr. 6436), BM(NH) (1989.623), and the USNMNH (242123). All the remaining specimens and exoskeletal parts are in the Frey collection in Bloomington.

Diagnosis. Presence of 10, 10, 7 and 5 spines in gnathobasic filter combs of limbs II-V and general morphology put this taxon in the genus Plurispina along with *P. chauliodus*. Animal almost as high as long; strong keel beginning immediately after posterior headpore; shell covered with radiating ridges; head and shell covered with densely packed tubercles, providing a marked opaqueness; ventral margin with mean of 122 marginal seta (n=6), terminating at a small triangular tooth, followed by submarginal row of small but blunt setae along posterior margin. Eight long swimming setae. Tip of rostrum bead-like. Labrum elongate and narrowly rounded at tip. Postabdomen elongate; preanal portion and anal groove subequal in length, both much shorter than postanal portion; ventral margin strongly flared out in anterior third; long slender marginal denticles, irregularly arranged, but few fine setae associated with them. Postabdominal claw rather thick, provided with a row of long, stout setae along concave margin; 2 basal spines, longer one about as long as basal width of claw, other one very slender and much shorter.

Parthenogenetic female. Shape and shell (Figs 376-378, 395-397). Almost as high as long; rostrum short; strong keel beginning immediately after posterior headpore (Fig.400). Shell covered everywhere with series of prominent radiating or sloping ridges (Figs 376-378, 395) and a reticulation-like pattern on head and shell; entire head and shell covered densely with rounded tubercles of various sizes (Figs 380, 396, 398, 400); these line up in rows along anterior ridges, producing an effect similar to striae in other species. Posterior-dorsal angle completely absent, i.e., no appreciable change in curvature; posterior-ventral angle weakly developed, with 1 or 2 small bluntly triangular denticles, followed by submarginal row of stout setules extending toward posterior-dorsal angle (Fig.397). Head in lateral contour bulged out slightly over compound eye, with noticeable expansion behind posterior pore (Fig.377), produced by beginning of keel. Ventral setae 122 (range 116-127, n=6), including 9-11 arising internally along line roughly paralleling anterior margin. Shell brownish in colour, relatively opaque from tubercles.

*Head* (Figs 379-381, 396, 398, 400). Rostrum about one third length of headshield (Fig.381); tip developed as small rounded point, somewhat separated from rest of rostrum (Figs 380, 398); edge rough from tubercles, but in plane view surface tubercles come out to row paralleling margin and do not occur between here and margin (Fig.380); no other markings; IP distance roughly 54  $\mu$ m; PP distance 6.8 times IP distance; minor pores only about 1 major pore diameter apart.

Antennule (Figs 379-381). Slender but rather short, and with rounded backward extension at base; 9 aesthetascs, about one third length of antennule; antennular seta about half as long as antennule, arises from a notch or cup about one third from tip; aesthetasc field surrounded by blunt triangles.

Antenna (Figs 381, 398). Formula: 0(1)-0-3(1)/1-1-

3(1). Eight long swimming setae; seta from basal segment of exopodite about two thirds length of longest natatory seta; 1 terminal seta from tip of each branch slightly shorter than other 2. Terminal spines on each branch long and well developed.

Labrum (Figs 382-387). Rather narrow blade, with tip moderately narrowed, rounded, not attenuated; anterior margin mostly evenly curved, sometimes with slight concavity or irregularity near tip; posterior margin usually weakly concave; angle considerably less than



**Figs 376-387.** *Plurispina multituberculata* n.sp. All specimens parthenogenetic PARATYPES from Bayly sample 66 (granite pool in Dutarning Range south of Perth, WA, 24 June 1977). 376. instar-I female; 377. parthenogenetic female; 378. shell of instar-I female; 379, 380. rostrum and antennules of parthenogenetic female (number 380 shows general distribution and size-range of tubercles near tip of rostrum); 381. headshield of parthenogenetic female, with antennule, antenna, and labrum (note change in curvature behind posterior headpore from initiation of keel); 382-387. labra of parthenogenetic females.

# 90°, rather narrow.

*Trunklimb I* (Figs 388, 389, 399). Two ODL and 3 IDL setae; long ODL seta and 2 long IDL setae about same length; smaller ODL seta less than half as long as basal segment of longer seta, seemingly without any brush-like setules in distal segment; smaller IDL seta apparently without setules; tip reaches setulate zone of other 2 setae; lateral seta arising near base of ODL-IDL

ridge well developed, openly brush-like. Accessory seta of middle and posterior groups of corm seta well developed; middle seta of middle group much the longest.

*Trunklimb II* (Fig.390). Ten setae in gnathobasic filter comb; all scraping spines with row of distinct spinules in distal segment; about 7 thick, curved setae between gnathobase and scraping spines.



Figs 388-394. *Plurispina multituberculata* n.sp. All specimens parthenogenetic PARATYPES from Bayly sample 66 (granite pool in Dutarning Range, WA, 24 June 1977). 388, 389. trunklimb I (NB: ODL2 is not feathered); 390. trunklimb II; 391. trunklimb V; 392. postabdomen of instar-I female; 393, 394. postabdomen of mature female.

*Trunklimbs III-V* (Fig.391). Ten, 7 and 5 setae in gnathobasic filter comb, respectively, and 7, 7 and 4 feathered exopodite setae. On trunklimb III, distalmost 2 'hard' setae slender, heavily chitinised, and either without setules or else extremely small; these project ventrally in intact animals. Soft setae of trunklimb IV close together, leaving long free margin on exopodite toward respiratory bulb.

*Postabdomen* (Figs 392-394, 401). Ventral margin straight distally, expanded outward at basal third; dorsal margin with both angles weak and almost absent; anal groove shallowly concave. Preanal portion and anal groove subequal in length, both much shorter than postanal portion. Postanal portion with irregular array of long slender denticles, which change orientation in basal half, creating confusing configuration; all thickly



**Figs 395-402.** *Plurispina multituberculata* n.sp. All specimens parthenogenetic PARATYPES from Bayly sample 66 (granite pool in Dutarning Range, WA, 24 June 1977). 395. parthenogenetic female; 396. shell-headshield junction, showing distribution of tubercles; 397. posterior-ventral angle and adjacent portion of posterior margin of shell, from inside; 398. rostrum and antennae; 399. trunklimb I, showing long but unfeathered ODL2 seta and relatively long IDL3 seta; 400. headpores and beginning of keel; 401. postabdomen; 402. tip of postabdomen and postabdominal claws.

chitinised, with few thin setae mixed in; often accessory denticles, sometimes arising laterally rather than with major denticles; no organisation into distinct groups of denticles, except occasionally basally, and these not positioned transverse to margin. Anal groove with 6 or 7 clusters of setae, each in a row, with tips extending well beyond margin, distalmost seta of each group thicker than other (Figs 393, 394); these probably derive from diagonal clusters of 2-3 seta each in instar-I individuals (Fig.392). Lateral surface of postanal portion with row of crescentic groups of setae, and with some additional groups distally, and along anal groove and in preanal region. Two curved rows of setules across ventral margin. Two or 3 weak indentations in distal part of preanal margin. Abdominal setae quite long, reaching to about two thirds of anal groove when extended.

*Postabdominal claw* (Figs 392-394, 402). Stout distally, with 2 successive rows of long, stout setae along concave margin. Two basal spines, longer one as long as basal width of claw, smaller one more slender, about half as long.

**Length.** Overall 0.50-0.88 mm (n=48); instar-I 0.50-0.59 mm (n=19); instar-II 0.61-0.72 mm (n=12); smallest female with eggs 0.73 mm.

## Pleuroxus helvenacus n.sp.

#### Figs 403-434

**Etymology.** From (L) *helvenacus* pale yellow, yellowish, from the general appearance of the specimens.

**Comments.** Although *Pleuroxus helvenacus* in many respects resembles the two species in the new genus *Plurispina* described in this paper, it is retained in the genus *Pleuroxus* because of its 8, 8, 6 and 4 setae in the gnathobasic filter combs of trunklimbs II-V, respectively.

**Material examined.** *Type locality.* Flooded meadow near Mount John, South Island, New Zealand, collected 20 Mar. 1987 by D.G. Frey, Frey accession number 8374. The meadow is 3.1 km from the highway along the road on the west side of Lake Tekapo.

Other locality. Tekapo pond 8A, in the same general region as type locality, collected 15 Oct. 1980 by C.W. Burns.

**Types.** All specimens and exuviae from the type locality, amounting to 19 specimens plus many shells and headshields with appendages. HOLOTYPE – a mature parthenogenetic female 0.74 mm long, mounted on a slide in glycerine jelly, NMNZ (Cr. 6437). PARATYPES – a mature parthenogenetic female on a slide in glycerine jelly has been deposited in each of the following museums: AM (P39482), BM(NH) (1989.624), and the

## USNMNH (242124).

All the remaining specimens and exoskeletal parts from the type series, plus 17 specimens recovered from the Tekapo pond, are in the Frey collection in Bloomington.

Short diagnosis. Almost as high as long; ventral margin weakly curved, provided with a mean of 118 marginal setae, those in posterior three fifths being densely feathered on outside; single rounded tooth (range 0-2) at posterior-ventral angle; entire shell and head covered with small rounded tubercles; about 8 short, curved striae at anterior end of shell; no keel present but instead a rather sharp ridge; light yellowish colour, without pigmentation. Labrum long, narrow, finely rounded at tip. Antennule slender, tapered to narrow tip; antennular seta arising one third from tip, longer than half of antennule; aesthetasc field surrounded by pyramidal tubercles. Antenna with 8 swimming setae, all almost equally long; basal segment and rami provided with transverse rows of spinules. Nothing distinctive about trunklimbs, except unusually long seta on exopodite of limb III. Postabdomen unique; about 20 marginal denticles or positions in postanal region, distally almost touching one another at base. proximally multiple, either as several equally developed denticles or 1 denticle and adjacent row of long setae; preanal length less than anal length, which is less than postanal; distal third of preanal portion single, with several chevron-like thickenings across margin; preanal angle reasonably distinct, postanal one obscured.

Parthenogenetic female. Shape and shell (Figs 403-405, 420, 427-430). Body almost as high as long; dorsal margin evenly curved from tip of rostrum to posteriorventral angle (posterior-dorsal angle almost completely absent); posterior margin short, weakly but evenly convex; ventral margin with weak bulge just anterior to midpoint, provided along entire margin with 118 setae (range 108-126, n=19), including about 12-15 long setae bent inward at anterior end (Fig.405), those in posterior three fifths strongly feathered laterally along posterior edge (Fig.430), those in anterior two fifths relatively unfeathered: about 8 short striae anteriorly, roughly paralleling anterior margin, with a series of radiating ridges posteriorly; most distinctive are the many fine tubercles scattered over entire shell (and head) (Figs 428, 429), sometimes organised into lines outlining meshes (Fig.405), as in central region of shell and along ventral edge; above tips of ridges and on head are many small depressions or dimples (Fig.428); dark line closely paralleling posterior margin (Fig.404). Generally 1 rounded tooth [0(4), 1/2(1), 1(28), 1 1/2(3), 2(9)] at posterior-ventral angle (Figs 404, 430), followed by row of marginal setae, which quickly become submarginal, extending toward posterior-dorsal angle. Body laterally compressed, narrow from side to side, tapering to a median ridge (not a keel) dorsally, beginning shortly behind head pores. Colour light yellowish, clear, no pigmentation.

*Head* (Figs 406-408). Headshield long, relatively narrow. Rostrum long, rather sharply tipped and with fine button-like extension; held close to body. IP distance averages 56  $\mu$ m; PP distance 5.4 times IP; minor pores

more than 2 pore diameters apart. Median longitudinal ridge beginning shortly behind headpores.

Antennule (Figs 409, 410, 431). Long, slender, tapered distally to narrow tip that is provided with pyramidal



**Figs 403-419.** *Pleuroxus helvenacus* n.sp. All specimens parthenogenetic PARATYPES from Frey sample 8374 (flooded meadow near Mount John, South Island, NZ, 20 Mar. 1987). 403. parthenogenetic female; 404. posterior-ventral angle and posterior margin of shell; 405. anterior portion of shell; 406-408. headshield; 409, 410. antennule; 411. exopodite of antenna; 412. endopodite of antenna; 413-419. labra.

tubercles at edge; base with a short backward expansion that is narrowly rounded at tip (Fig.431). Nine slender aesthetascs, about one third length of antennule; antennular seta half as long as antennule, arising one third from tip. Antenna (Figs 411, 412). Eight long swimming setae, the one from basal segment of endopodite almost as long as others; one of terminal setae on each branch only very slightly shorter than other 2; all basal segments provided with numerous setules laterally. Terminal spines



Figs 420-426. *Pleuroxus helvenacus* n.sp. All specimens parthenogenetic PARATYPES from Frey sample 8374 (flooded meadow near Mount John, South Island, NZ, 20 Mar. 1987). 420. shell; 421, 422. trunklimb I; 423. gnathobase and three scraping spines of trunklimb II; 424. trunklimb III, showing the one very long exopodite seta; 425, 426. postabdomen and postabdominal claw.

less than half length of terminal segments; spine from basal segment of exopodite very small. All segments of both branches of antenna with transverse median and distal rows of fine spinules.

*Labrum* (Figs 413-419). Labral keel elongate, tapered to narrow, rounded tip; anterior margin relatively straight toward tip, sometimes with notch or waviness near tip;

posterior margin usually weakly concave, sometimes almost straight; posterior angle narrow, considerably less than  $90^{\circ}$ .

Trunklimb I (Figs 421-422). Two ODL setae, smaller one short but distinct, unfeathered; 3 IDL setae, shortest one evenly tapered, bluntish at tip, not reaching distal ends of basal segments of 2 long setae. Middle



**Figs 427-434.** *Pleuroxus helvenacus* n.sp. All specimens PARATYPES from Frey sample 8374 (flooded meadow near Mount John, South Island, NZ, 20 Mar. 1987). Specimen 432 is an ephippium, all others mature parthenogenetic females. 427. parthenogenetic female; 428. dimples and tubercles at shell-headshield boundary; 429. headpores and tubercles (note distance apart of minor pores); 430. posterior-ventral angle with tooth, plus shell margin and setae on either side; 431. antennules (note backward extension at base); 432. ephippium; 433,434. postabdomen and postabdominal claws (note that distal denticles on postabdomen are all single and close together).

seta of middle group of corm setae much the longest. All 3 accessory setae well developed. Long, delicate lateral setae arising laterally from base of ODL-IDL ridge.

*Trunklimb II* (Fig.423). Short seta on margin between gnathobasic setae and scraping spines, with 2 long setae toward gnathobasic setae, and 7 or 8 stout curved setae toward scraping spines. Scraping spines 1-3 considerably shorter than number 4; first 7 setae provided with row of slender setules along distal segment; 8 setae in gnathobasic filter comb.

*Trunklimbs III-V.* Setae in gnathobasic filter comb number 8, 6 and 4 (3 in one specimen), respectively, and number of soft setae on exopodite 7, 7 and 4, respectively. No striking differences in morphology, although longest exopodite seta of limb III is longer than usual (Fig.424).

Postabdomen (Figs 425, 426, 433, 434). Elongate and broad; preanal portion less than anal portion which is less than postanal. Ventral margin flared outward proximally, 2 curved rows of spinules embracing margin. Postanal margin with about 20 denticles or denticle positions; distal denticles almost touching at bases; proximal ones multiple, either as several strong setae or as one or a couple strong setae distally and several long setae proximally; anal groove armed with about 7 successive groups of long setae, each group typically ending in a stouter seta distally, and all groups tending to project well beyond margin; single row of spinular crescents laterally along dorsal margin, with a few additional groups distally, and many additional groups proximally and in preanal region. Preanal angle reasonably distinct; postanal angle obscure, rounded. Several transverse, chevron-like folds in distal third of preanal region; proximal two thirds expanded somewhat laterally. Abdominal setae quite long, reaching to about middle of anal groove when extended.

*Postabdominal claw* (Figs 425, 434). Slender; evenly tapered and evenly curved. Two basal spines, longer one curved outward away from claw, longer than basal width of claw, shorter one straight, more slender, about half as long. Row of long setae along concave margin, plus row along medial surface that project beyond concave margin.

**Ephippium** (Fig.432). Just one ephippium was found, which is typical for the chydorine anomopods in its morphology. Anterior and ventral parts of shell that peel away from ephippium anteriorly remain broadly attached near posterior end. Surface sculpturing a series of angular tubercles, each with several lines or ridges radiating outward.

Length. Type population. Overall 0.52-0.88 mm (n=19); instar-I 0.52-0.60 mm (n=10); mature 0.73-0.88 mm (n=9); smallest female with eggs 0.76 mm. Tekapo pond 8A: overall 0.57-0.89 mm (n=17); instar-I 0.57-0.59 mm (n=3); instar-II 0.62-0.71 mm (n=6); mature 0.76-0.89 mm (n=8); smallest female with eggs 0.78 mm.

## Planicirclus n.gen.

Type species. *Planicirclus alticarinatus* n.sp. by original designation.

**Etymology.** From (L) *planus* flat, and (L) *circlus* a circle or circular body (masculine gender), referring to the general shape of the taxon.

**Remarks.** This taxon from Western Australia is by far the largest in size among the Pleuroxus-like group of species. Many of its characters that seem unique may be related to its large size. Thus, the PP distance is extremely long - about 13 IP distances; the ventral setae on the shell average 186, which is much greater than for any other species; the eye and ocellus are very small relative to the size of the animal and are very close together; and there are up to 25 curved striae in the anterior part of the shell, many more than in any other species. On the other hand, there are some truly distinctive characters: there is a long secondary seta on the ODL, longer than in Plurispina, which is strongly brush-like in the distal segment; the middle and posterior setae of the middle group of corm setae are almost equally long, the middle seta being only slightly longer; there are very many setular crescents on the sides of the postabdomen; and there are two resting eggs in the ephippium. The setae on the gnathobasic filter comb of trunklimbs II-V number 8, 8, 6 and 4, respectively, which is typical for most Pleuroxus and Pleuroxus-like species from Australia and New Zealand. Deciding which of these characters are generic characters will have to await the finding of a second species in the genus. The taxon seems most closely related to Pleuroxus helvenacus from New Zealand in the shape of the postabdomen and its large number of marginal denticles, and in the regular, attenuated shape of the labrum, but the smaller ODL seta of Pleuroxus helvenacus is much different, and the middle seta of the middle group on the corm is much the longest. Resolution of the significance of these similarities and differences will have to wait until males and ephippial females of the New Zealand taxon become available.

#### Planicirclus alticarinatus n.sp.

# Figs 435-488

**Etymology.** From (L) *altus* high, deep, and (L) *carina* a keel, referring to the broad keel on the head and shell.

**Material examined.** *Type locality.* Cracker's Swamp, 210 km north of Perth and 4.8 km west of Brand Highway, collected by R.J. Shiel on 30 Sept. 1981, his accession number 792 (field number W.A. 4). Dark

humic water, less than 30 cm deep. Conductivity 800  $\mu$ S cm<sup>-1</sup>

**Types.** 111 specimens, plus numerous heads, shells, and some exuviae from type locality. HOLOTYPE – a mature parthenogenetic female 1.23 mm long,

mounted on a slide in glycerine jelly, AM (P39483). ALLOTYPE – a mature male 1.07 mm long, mounted on a slide in glycerine jelly, AM (P39484). Special PARATYPES – mounted separately on slides in glycerine jelly, AM: an ephippial female 1.37 mm long (P39485); an instar-I male 0.75 mm long (P39487); an



Figs 435-442. *Planicirclus alticarinatus* n.sp. All specimens PARATYPES from Shiel sample 792 (Cracker's Swamp, 210 km north of Perth, WA, 30 Sept. 1981). 435. parthenogenetic female; 436. ephippial female (note two ephippial eggs); 437. 438. trunklimb I, showing subequal lengths of middle and posterior setae of middle group of corm setae, and large size and brushy distal segment of ODL2; 439, 440. rostrum, with button-like tip; 441, 442. postabdomen of parthenogenetic female.

instar-II male 0.87 mm long (P39486). PARATYPES – 1 slide each containing a mature parthenogenetic female, an ephippial female, an instar-I male, an instar-II male, and a mature male, mounted separately in glycerine jelly, have been deposited in the following museums. The numbers are the catalogue or registration numbers of the specimens.

	NMNZ	BM(NH)	USNMNH
Paratypes			
parthenogenetic female	Cr. 6438	1989.625	242125
ephippial female	Cr. 6439	1989.627	242125
instar-I male	Cr. 6440	1989.629	242125
instar-II male	Cr. 6441	1989.628	242125
mature male	Cr. 6442	1989.626	242125



Figs 443-458. *Planicirclus alticarinatus* n.sp. All specimens PARATYPES from Shiel sample 792 (Cracker's Swamp, 210 km north of Perth, WA, 30 Sept. 1981). 443. instar-II male; 444. mature male; 445-452. labra of parthenogenetic females; 453, 454. bifid rostrum of instar-II male, with antennules and antenna; 455-457. headshield and rostrum with bifid button, mature male; 458. trunklimb IV of parthenogenetic female.

All the remaining paratypes are in the Frey collection in Bloomington.

circular in lateral outline, laterally compressed, with a high keel beginning just behind headpores, and with rostrum held close to body. PP distance very long, averaging 12.6 times IP distance. Mean of 186 ventral



**Figs 459-467.** *Planicirclus alticarinatus* n.sp. All specimens PARATYPES from Shiel sample 792 (Cracker's Swamp, 210 km north of Perth, WA, 30 Sept. 1981). 459. antennule of instar-II male (note that anlage of male seta, M', is short and stout; antennular seta, AS, is long and arises only about 1/5 from end); 460. part of trunklimb I of instar-I male (CH', anlage of copulatory hook; ODL2, shorter seta of ODL, which in this species is very long and highly brush-like in the distal segment); 461. part of trunklimb I of instar-I male; 463, 464. postabdomen of instar-II male; 465-467. postabdomen of mature male.

setae on shell, including those turned inward at anterior end. Entire surface of shell covered with ridges, cross connections, and scallops; about 15-25 anterior ridges paralleling anterior margin, with short striae. ODL has long second spine, strongly plumose in distal segment, as long as basal segment of longer ODL spine. Antennular seta long, arising one quarter from tip of antennule. Eight long swimming setae on antenna, shortest from basal segment of endopodite. Postabdomen with anal groove deeply concave, shorter than preanal and postanal portions, which are roughly subequal; postanal portion with about 20 denticles or denticle positions; denticles long, slender, somewhat curved toward anal groove, distal denticles close together at their bases; many spinular crescents along sides of postabdomen, particularly along anal groove and in preanal region; 2 crescents of fine setae across ventral margin of postabdomen. Setae in gnathobasic filter combs number 8, 8, 6 and 4 in limbs II-V, respectively. Males almost as nearly circular in outline as females. Instar-II male with stout anlage of male seta on antennule, arising about one third from tip; rostrum shorter and broader than in female, with two small denticles at tip. Mature male has long, brushy male seta on antennule; rostrum short, truncate, and with small emarginate globule arising subterminally at tip; anterior part of ventral margin of shell turned inward, with many long, very slender setae seeming to arise directly from shell; postabdomen more



**Figs 468-474.** *Planicirclus alticarinatus* n.sp. All specimens PARATYPES from Shiel sample 792. 468. parthenogenetic female; 469. anterior view of parthenogenetic female, showing rostrum, antennae, and strong keel beginning just behind posterior median pore; 470. sculpturing of shell of parthenogenetic female; 471. posterior-ventral region of shell of parthenogenetic female, showing complete absence of any denticle; 472-474. postabdomen and postabdominal claws.

slender and elongate than in female; preanal angle sharp but very obtuse, and postanal angle rounded and inconspicuous; denticles mostly multiple, with groups arranged transversely or obliquely to margin; genital pore far distad, near base of peduncle for claw.

**Parthenogenetic female.** Shape and shell (Figs 435, 468-471). Disc-shaped, almost circular in lateral view, with ventral margin having much less curvature than dorsal margin; body strongly flattened from side to side, and with very sharp keel beginning directly behind posterior pore and continuing to posterior-dorsal angle. Series of 15-25 short, vertical striae on anterior part of shell, roughly paralleling anterior margin; elsewhere on

shell are various ridges and reticulations - longitudinal ridges dorsally, reticulations ventrally and posteriorly; ventral portion of shell with irregular dimples and ridges; a mean of 186 marginal setae (range 167-203, n=20), including specimens of all stages and instars except mature males), including 10-12 at anterior end that turn inward from submarginal ridge; no tooth at posterior-ventral angle in any specimens (Figs 471, 482), but row of slender and short marginal-submarginal setae along posterior margin to posterior-dorsal angle. Shell surface irregularly dimpled (Fig.470). Rostrum held close to body; antennules and part of labrum obscured by antennae directed downward.

Head (Figs 439, 440, 469). Strongly convex, with



**Figs 475-479.** *Planicirclus alticarinatus* n.sp. All specimens PARATYPES from Shiel sample 792. 475. ephippial female (note distinctness of slough line); 476. instar-II male; 477. postabdomen of mature male; 478, 479. tip of postabdomen and postabdominal claws of mature male (note distinct angle at the ventral tip of the caudal peduncle, and long, straight nature of basal spines).



Figs 480-488. *Planicirclus atlicarinatus* n.sp. All specimens PARATYPES from Shiel sample 792. 480. ephippium; 481. frontal view of instar-II male, showing rostrum and long terminal setae on antennal branches; 482. posterior-ventral region of shell of instar-II male, showing ventral setae and posterior setules unseparated by any denticle; 483. trunklimb I of instar-II male (LS, lateral seta; ODL2, long, feathered lesser ODL seta; CBS', anlage of copulatory brush seta; MS', anlage of male seta on IDL); 484. antennules of instar-II male; 485. antennule of mature male (note long and brushy male seta, M, and far distal origin of antennular seta, AS; aesthetascs are relatively short); 486, 487, postabdomen and postabdominal claws of instar-II male (long, slender and relatively straight basal spines are noteworthy); 488. postabdomen of mature male.

strong keel behind pores; cannot be spread flat without generating excessive folding; narrowed posteriorly and somewhat truncate in lateral view where it meets keel of shell (Fig.435). Rostrum rather short and broad (Fig.439), tapered to a bubble-like tip (Fig.440). IP distance about 60  $\mu$ m (n=10); PP distance averages 12.6 times IP distance. Eye slightly larger than ocellus, but both small relative to size of animal and close together; distance from ocellus to tip of rostrum many times greater than distance between eye and ocellus; both placed some distance from margin.

Antennule. Elongate; antennular seta almost as long as antennule, arising about one quarter from tip; 9 aesthetascs, about one third length of antennule; rounded expansion at base projecting backward.

Antenna (Figs 453, 484). Formula: 0(1)-0-3(1)/1-1-3(1). Eight long swimming setae; seta arising from basal segment of endopodite more than half as long as other seven; terminal spines long, about as long as segments from which they arise; spine from basal segment of exopodite well developed; rows of spinules on all segments of both rami and on basal segment (Fig.484).

*Labrum* (Figs 445-452). Anterior margin evenly curved to narrow tip, usually with slight concavity just before tip; posterior margin concave, usually irregularly so; posterior angle rather narrow, considerably less than 90°.

*Trunklimb 1* (Figs 437, 438). ODL with 2 setae, smaller one as long as basal segment of longer seta, with many setules arising from distal segment, giving it a brush-like appearance; longer seta with no setules visible with 40x phase objective. IDL with 3 setae, shortest stout to tip and apparently without setules, about as long as basal segment of the other 2; these have rows of long setae anteriorly along distal segment. Middle and posterior setae of middle group of corm setae almost equally long, middle seta slightly longer; well developed feathered and delicate lateral seta arising near base of ODL-IDL ridge (Fig.403).

*Trunklimbs II-V* (Fig.458). Setae in gnathobasic filter combs number 8, 8, 6 and 4 on limbs II-V, respectively; 7, 7 and 4 soft setae on limbs III-V, respectively. Otherwise morphology typical of *Pleuroxus* group. All scraping spines of limb II with fine spinules along distal segment.

Postabdomen (Figs 441-442, 472-474). Anal groove strongly concave; preanal angle well developed, somewhat rounded; postanal angle less strong and broadly rounded. Anal groove shorter than preanal portion, which in turn is slightly shorter than postanal; latter tapers distally to rounded distal angle. About 20 marginal denticles or denticle positions; denticles very long, slender, slightly curved; distal denticles single, tightly packed together at bases; proximal denticles with varying number of subdenticles and setae associated; anal groove with 6-7 sequential rows of setae projecting beyond margin. Preanal portion single in distal quarter, with about 4 or 5 transverse ridges, which show up as scallops from side; expands somewhat from side to side proximally. Lateral surface with 2 rows of spinular crescents along postanal portion and along distal part of anal groove; complex arrangement of very many rows of crescents in anterior two thirds of anal groove and in preanal portion. Abdominal setae rather short, barely reach anal groove when extended. Ventral margin long and with distinct break in curvature about one third from proximal end, producing a pronounced bowing outward; 2 angular rows (or crescents) of fine spinules across ventral margin.

*Postabdominal claw* (Figs 441, 442, 474). Long, slender; evenly but weakly curved to bluntish point at tip; concave margin provided with 2 sequential rows of setules, proximal row with longer ones; median surface with row of setules toward convex margin, which project beyond margin irregularly. Two long basal spines, longer one slender, considerably longer than basal width of claw; shorter one even more slender, straight, length about equal to basal width of claw.

**Ephippial female** (Figs 436, 475, 480). Two resting eggs in all ephippial females (Fig.436) and ephippia. Lining of broodpouch heavily pigmented, and pigmentation also in ephippial part of shell, sometimes so heavy it obscures all details beneath. Slough line sharply evident, beginning just posterior to mandibular articulation and then proceeding ventrally and posteriorly toward posterior-ventral angle; junction between ephippium and ventral margin of shell so broad that shell flaps seldom slough off completely (Fig.480). Dorsal margin heavily chitinised within keel. Surface of ephippium with angular tubercles of different sizes.

Male. Males show the 3-instar ontogeny characteristic of all chydorids known to date. These include shortening and rounding of the rostrum; thickening of the antennule, development of a long male seta, and often with more than 9 aesthetascs, which are difficult to count; development of copulatory hook, copulatory brush, copulatory brush seta, and male seta on trunklimb I; and often in changes in shape and armament of the postabdomen and the postabdominal claw. All three instars have much the same shape as females - thin, highly arched, almost circular from the side, and with no posterior-dorsal and posterior-ventral angles (break in curvature) on shell.

*Instar-I* (Figs 460, 462). Copulatory hook peg-like; no anlagen of any other setae. Postanal portion of postabdomen shortened, so that all 3 zones subequal in length; stout setae along anal groove where rows of setae develop in instars II and III, and greatly reduced number and development of spinules laterally as compared with female. Genital pore small, located near ventral margin at distance equal to half length of claw.

Instar-II (Figs 438, 443, 453, 454, 459, 461, 463, 464, 476, 481-484, 486, 487). Copulatory hook angular and J-shaped (Figs 443, 461, 483). Anlage of male seta on antennule short, stout, weakly divided into 2 segments, arising one third from end of antennule (Fig.459); antennular seta long and slender arising about one third from end. Anlagen of male seta on IDL and of copulatory brush seta. Rostrum shorter and broader than

in female (compare Figs 469 and 481), and although bluntly pointed has 2 small denticles at tip (Figs 453, 454). Postabdomen similar to female in general shape, proportions, and armament, except that ventral margin more strongly expanded basally (Figs 463, 464); marginal denticles nearly all single and with few complications from accessory denticles or spinules; genital pore slightly farther distally than in instar-I and usually with a thin sperm duct coming to it. Postabdominal claw same as in female.

*Mature* (Figs 444, 455-457, 465-467, 477-479, 485, 488). Copulatory hook long, slender, U-shaped, with 3 crescentic ridges crosswise near tip. Male seta on antennule almost as long as antennule, strongly plumose in distal segment (Fig.485); number of aesthetascs indistinct, but seemingly fewer than 12 and possibly only 10. On trunklimb I male seta long and curving forward; copulatory brush a small discrete group of long setae; copulatory brush seta large, elongated, distal segment thin and mostly obscured by copulatory brush. Rostrum short, broad, truncate and weakly rounded at tip, provided with a globular tubercle that is distinctly emarginate,

arising subterminally from underside (Figs 455-457); dorsal surface sunken dish-like, so that margin distinctly higher than centre. Postabdomen more elongate and more slender than in instar-II male or female and with a suppressed postanal angle (Figs 465-467, 477-479); crescents and rows of spinules laterally have about same arrangement as in female, but marginal denticles nearly all multiple and arranged in transverse or oblique clusters; genital pore located far distally near base of peduncle for claw (Figs 478, 479); distinct angle at distal end of peduncle ventrally. Postabdominal claw somewhat shorter, stouter, and seemingly slightly more curved than in female. On shell anterior to midventral bulge shell margin rolled inward, and marginal seta, therefore, turned inward; many very slender and long setae here arise from turned-in margin and project ventrally, producing a brushy appearance (Fig.444).

**Length.** Females: overall 0.81-1.75 mm (n=45); first eggs at 1.21 mm; ephippial 1.35-1.68 mm (n=14). Males: instar-I 0.75-0.86 mm (n=12); instar-II 0.82-0.97 mm (n=20); mature 0.93-1.10 (n=20).

# Artificial Key to Populations of *Pleuroxus* and *Pleuroxus*-like Taxa Known from Australia and New Zealand as Treated in this Paper

*Pleuroxus aduncus*, which is redescribed in this paper, is not included in the key, because it does not occur in Australia. *Pleuroxus laevis* Sars, *Pleuroxus denticulatus* Birge and *Pleuroxus similis* Vavra likewise are not included, nor are the six taxa described by Smith and Henry from the region of Sydney. The latter will be considered in a subsequent chapter. It is certain that more, possibly many more, species of *Pleuroxus* and related genera will be distinguished, particularly in Western Australia, as the weakly saline, minute, and ephemeral waterbodies are studied more closely.

1.	Shell and head covered with small rounded tubercles2
	Shell and head without rounded tubercles4
2.	Setae in gnathobasic filter combs on trunklimbs II-V number 8, 8, 6 and 4, respectively; no sharp keel on head behind pores and on shell; about 20 postabdominal denticles, distal ones almost touching at their bases <i>Pleuroxus helvenacus</i> n.sp.
	Note: This taxon is known only from New Zealand. It has an average of 118 ventral setae on the shell, including the 10 or so at anterior end that arise submarginally and project centrally, rather than outward. Labrum long and narrow. Single small rounded denticle (range 0-2) at posterior-ventral angle of shell. PP distance averages 5.4 times IP distance.
	Setae in gnathobasic filter combs on trunklimbs II-V number 10, 10, 7 and 5, respectively; sharp keel dorsally behind posterior headpore; about 12-15 postabdominal denticles

3.	Preanal portion of postabdomen much shorter than anal portion, which is about equal to postanal portion; tip of rostrum weakly bifid; tubercles on shell moderately dense
	Note: The male of this taxon is highly distinctive, with 2 strong, tusk-like denticles arising submarginally from tip of rostrum, and with the distal segment of the male seta on the antennule strongly brush-like. Shorter seta on ODL also strongly brush-like. About 107 ventral setae on shell. PP/IP ratio about 7.6. Spines on claw very short, longer spine less than width of claw.
	Preanal portion of postabdomen about equal in length to anal portion, and both much shorter than postanal portion; tip of rostrum beadlike; tubercles on shell larger and densely packed, producing a general opacity 
-	Note: Entire shell covered with radiating ridges and deep troughs separating them; no actual striae on shell, these being approximated by rows of tubercles. Shorter seta on ODL without brush-like setation. About 122 ventral setae on shell. PP/IP ratio 6.8.
4.	Length of anal portion less than that of preanal and postanal; 2 resting eggs
	Length of anal portion about equal to preanal, and both less than postanal; 1 resting egg
5.	About 90 setae on shell; PP/IP ratio about 4.7; polyembryonic
	Note: In addition, Archepleuroxus has about 12 denticles on the postabdomen, usually no tooth on the shell although occasionally one very small tooth. The postabdominal claw of the male is shorter than in the female and is somewhat sigmoid.
	About 180 seta on shell; PP/IP ratio about 12.6; only 2 parthenogenetic eggs
	Note: This is by far the largest species of the group, and the largest chydorid known outside the two genera <i>Eurycercus</i> and <i>Saycia</i> . It reaches a length at least up to 1.75 mm. The species is almost circular in shape and strongly flattened. It has a very sharp keel on the shell, the latter being covered with radiating ridges. No tooth is present. The postabdomen has about 20 marginal denticles, closely packed distally, and has many crescents of setules laterally in the anal and preanal portion. The middle and posterior setae of the middle group of corm setae are almost equally long. The distal segment of the male seta on the antennule is strongly brush-like.

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6.	Surface of shell and head behind pores covered with small dimples; about 100 ventral setae on shell; PP/IP ratio mostly about 6; strong tendency toward 9 setae in gnathobasic filter comb of trunklimb III
	<b>Note:</b> The shell is weakly ridged, there is a small triangular tooth on the shell, and the preanal and anal portions of the postabdomen, which are roughly equal in length, are much shorter than the postanal portion. The shell flaps of the ephippium are only narrowly attached posteriorly, and hence can easily be sloughed off after molting.
	Surface of shell smooth, without dimples; mostly fewer than 90 ventral setae on shell; PP/IP ratio less than 4; 8 setae in gnathobasic filter comb of trunklimb III
7.	Eight to 10 marginal denticles, all multiple; distinct, sharply pointed tooth on shell
	<b>Note:</b> This taxon is from New Zealand. It has 80 or fewer ventral setae on the shell, a PP/IP ratio of less than 3, and the male has 9 transverse rows of the same size setae on the postabdomen, none in any rows sufficiently larger than the others to be considered a denticle.
	Twelve to 13 marginal denticles, distal ones simple; no tooth on shell or else a very small one
	Note: This is the commonest species of Pleuroxus in

Note: This is the commonest species of *Pleuroxus* in southern Australia. It is well defined by the various characters used in the key.

# Other Taxa

Besides the nine taxa considered in detail in this paper, Table 1 lists three taxa described from other continents, a taxon described by Smith (1909) from Tasmania, and five by Henry (1918, 1922) from New South Wales. The six taxa from Australia were judged to be possible members of the *Pleuroxus* group, either because of the generic name used by the describers or because of their morphology. The latter in all instances is inadequately described and illustrated for our present needs. An attempt was made without success to locate specimens of Smith's taxon, but type specimens of all of Henry's taxa except Pleuroxus reticulatus were borrowed from the Australian Museum. In addition, three specimens from Australia labelled Pleuroxus aduncus and three labelled Pleuroxus denticulatus were borrowed.

The three specimens labelled *Pleuroxus aduncus* are probably *P. inermis* instead. The three specimens labelled *Pleuroxus denticulatus* are not all from the same taxon: one resembles Henry's *Pleuroxus australis*, the other two have a *Pleuroxus laevis*-type postabdomen, and none of them is Birge's *Pleuroxus denticulatus*. No specimens of *Alonella nasuta* were available, and hence the taxon could not be evaluated properly. *Pleuroxus* reticulatus belongs in two other genera. Chydorus denticulatus seems quite certainly to be *Pleuroxus* inermis. The holotypes of Henry's *Pleuroxus* australis, Chydorus unispinus and Chydorus jugosus are all properly in *Pleuroxus*, but insufficient evidence can be discerned to determine, especially for Chydorus jugosus, to which taxa they correspond. In addition to Alonella nasuta, Henry's species must therefore be nomina dubia at present. This illustrates strikingly the insufficiency of single specimens to characterise a taxon. Populations containing diverse instars and stages must be available for a reasonable understanding.

1. *Pleuroxus aduncus* (Jurine, 1820). This taxon described from France is now known not to occur in Australia. Three specimens collected by B.V. Timms and so labelled are in the AM. All specimens are mounted in a medium with poor refractive index for resolving fine details.

a. *Slide P34983*. Mount House Station, Kimberleys, 4 Oct. 1982. (BVT?). Parthenogenetic female without eggs, length 0.51 mm. Body quite high, tapered downward posteriorly to a posterior-dorsal angle that is distinct; posterior-ventral angle more rounded, contains a small tooth on one side only. About 77 ventral setae on shell,

excluding any internal setae at anterior end. Ventral portions of about 9 curved striae visible in anterior part of shell. Ocellus and eye about equal in diameter. Rostrum short. Labrum rather short and broad, tip narrowly rounded. IP distance 56  $\mu$ m, PP 189  $\mu$ m, PP/ IP ratio 3.4. Postabdomen: anal region = preanal which is less than postanal; broad, tapered distally and rounded somewhat at end; denticles cannot be counted, and lateral crescents not visible.

This specimen is probably *Pleuroxus inermis* Sars, 1896.

b. *Slide P34985*. Richmond, Qld, 10 July 1984. BVT. Parthenogenetic female with 2 early embryos, length 0.48 mm. Body reasonably high, sloping down to short posterior margin, with a slight concavity just before posterior-dorsal angle. Posterior-ventral angle narrowly rounded, and with 1 small but distinct tooth at change in curvature. Postabdomen: preanal portion less than or equal to anal which is less than postanal; armature visible only vaguely - possibly 10-12 long, slender denticles. Both basal spines of claw long, longer one slender and curved away from claw, smaller one straight and slender, both equal to or slightly greater than basal width of claw. Eye slightly larger than ocellus. Headpores not visible. Other details obscure.

This specimen is probably *Pleuroxus inermis* Sars, 1896

c. *Slide P34984.* Palm Valley, NT, 25 June 1981. BVT. Parthenogenetic female with 2 early embryos, length 0.49 mm. Poor resolution from mounting medium, so that most details only vaguely perceivable at best. Seems to share many of the details of the previous specimen, although anal groove is relatively longer, and there are 2 teeth on 1 valve, one on the other. The shape of the animal is much the same as for the 2 previous specimens, with a rather short rostrum and reasonably distinct posterior-dorsal and posterior-ventral angles.

This specimen is possibly *Pleuroxus inermis* Sars, 1896.

None of these specimens is *Pleuroxus aduncus* (Jurine, 1820), and with the scarcity of details it is quite impossible to tell what they are. They are most closely related to *Pleuroxus inermis*, as defined in the present study, but the rostrum is somewhat shorter, the labrum more broadly expanded, and the count of ventral setae on the shell smaller than is characteristic of *P. inermis*. Possibly they represent an undescribed species.

2. Pleuroxus denticulatus Birge, 1879. The three specimens so labelled in the AM were also collected and mounted by B.V. Timms. Although no taxa in the *Pleuroxus laevis* group or *Pleuroxus denticulatus*-group were treated in this paper, the specimens were examined cursorially.

a. *Slide P27722*. Keil's Dam via Macksville, NSW, 24 Aug. 1967. (BVT?). Parthenogenetic female with 2 advanced embryos, length 0.39 mm. Rather elongate and not overly high; both posterior-dorsal and posterior-ventral angles distinct; 2 broad-based triangular teeth on each valve; only 64 ventral setae on shell, not counting any interior setae at anterior end, which were not visible.

IP distance 54  $\mu$ m, PP 124  $\mu$ m, PP/IP ratio 2.3. Postabdomen: anal region less than preanal which is much less than postanal; general shape somewhat similar to *Pleuroxus denticulatus*: both dorsal and ventral margins straight, tapering distally to acutely truncate distal end; possibly 12 or 13 denticles, rather stout, all single distally but proximal ones with short rows of setae proximally. Postabdominal claw long, slender; basal spines quite straight, longer one a little longer than basal width of claw, shorter one less than half as long. Specimen mounted in balsam, but obscured by being at edge of coverglass.

This specimen definitely is not the same as Birge's P. *denticulatus*. It resembles *Pleuroxus australis* in the general shape of the postabdomen and in the nature of the teeth on the valves.

b. Slide P34988. Mataranka, NT, 13 July 1981. BVT. Parthenogenetic female without embryos, length 0.40 mm. Body quite low, and dorsal margin slightly concave before posterior-dorsal angle, as in *P. aduncus*. Posteriorventral angle well formed, with 3 broad-based, pointed teeth on each valve; 76 ventral setae, not counting any interior setae forward. Rostrum long, slender, bent posteriorly and tucked against body. Eye larger than ocellus. Postabdomen similar to that of *P. laevis* in shape: anal portion less than preanal which is much less than postanal; about 12 marginal denticles, all single, straight, slender, and well separated from one another. Postabdominal claw with longer basal spine straight and considerably longer than basal width of claw, shorter one much less than half as long. Other details obscure.

c. Slide P34989. Kaban, Qld, 18 July 1983. BVT. Parthenogenetic female with 2 embryos, length 0.43 mm. Ventral margin convex; dorsal margin high but bending down sharply to indistinct posterior-dorsal angle; posteriorventral angle about 90°, narrowly rounded, with 3 broadbased and pointed teeth at lower edge of posterior margin; ventral setae 79, not counting any anterior setae, which were not visible; no curved striae visible on shell anteriorly and no shell markings. Eye almost twice size of ocellus. IP distance 61 µm, PP 142 µm, PP/IP ratio 2.3. Postabdomen of *P. laevis* type: anal region less than preanal which is much less than postanal; ventral margin gently and evenly convex; dorsal margin essentially straight, or even a little concave, provided with about 12 short, slender, pointed, well-separated denticles, only a couple of the proximalmost ones not being single. Postabdominal claw slender; longer basal spine slender and curved outward, considerably longer than basal width of claw; smaller one very slender, less than half as long as longer ones. Other details obscure.

None of these three specimens is any of the nine species considered in detail in this paper, and none of them is P. *denticulatus* Birge. Moreover, it seems quite certain that they are not all from the same taxon. As it is impossible to describe a species from a single specimen, even when details are clear, identification will have to wait until large populations containing males and ephippial females become available.

3. Alonella nasuta Smith, 1909: 84, pl.16, figs 4,5.
No specimens could be located in the AM or in the Hope Collections at Oxford University, the latter of which contains specimens of some of the other taxa Smith described in this paper. Hence the following comments are based entirely on Smith's description.

The illustration suggests this taxon might belong to the Pleuroxus group. The animal has a long, bluntlytipped rostrum, and the carapace has a series of radiating striae (or ridges) everywhere except in the anterior-dorsal region. The carapace is described as 'regularly oval without any marked angles', although the figure shows a change in curvature posteriorly, which is probably the posterior-dorsal angle. The postabdomen is *Pleuroxus* in shape, with four 'stout short spines' distally along the postanal margin and five 'groups of bristles' anterior to these. The length is given as 0.5 mm, which puts this among the smaller *Pleuroxus* taxa. Smirnov & Timms (1983) list this taxon as a synonym of P. aduncus, which is unrealistic because of the markings on the carapace, the lack of any teeth at the posterior-ventral angle, and the single distal denticles on the postabdomen.

The taxon at present must be considered a nomen dubium.

4. Pleuroxus reticulatus Henry, 1918: 478-479, pl.42, figs 13,14. The taxon illustrated here is a species of *Alonella*, most likely *A. clathratula*, but the specimen deposited as the holotype and the taxon illustrated in Henry (1922) are considered to be in a new genus by Smirnov, listed as *Monoporus* in Smirnov (1977) but changed to *Monope* by Smirnov & Timms (1983), the name of the taxon now being *Monope reticulata* (Henry, 1922). The 1918 description is of the *Alonella* taxon. It is much smaller than *Pleuroxus* or *Monope*, being listed as only 0.31 mm.

5. Chydorus denticulatus Henry, 1918: 480-481, pl.42, figs 15,16. Slide P4334 = HOLOTYPE. Parthenogenetic female with 2 eggs, length 0.60 mm. Body highly arched, with quite a distinct posterior-ventral angle and less distinct posterior-dorsal angle; each valve has a small tooth at posterior-ventral angle; 8 or 9 curved striae anteriorly, which bend posteriorly at bottom and join a stria continuing posteriorly close to ventral margin; no other shell markings apparent; 92 ventral setae on left side, including about 8 submarginal setae at anterior end, and 83 on right side, not including any of these anterior setae; no keel. Rostrum quite short. IP distance 54 µm, PP 224 µm, PP/IP ratio 4.1. Terminal spines on antenna very short; any spine present on basal segment of exopodite obscured by debris. Postabdomen: anal region less than preanal which is less than or equal to postanal; 13 postanal denticles, all multiple except for a few of the distalmost ones. Postabdominal claw with 2 basal spines, longer of which is considerably longer than basal width of claw, slender, and curved away from claw. According to Henry, the carapace is marked by small pits, which become larger and more conspicuous dorsally. Henry also states that there are 16 groups of spines along the postanal margin of the postabdomen and that the length of the taxon is 0.46 mm. These are seemingly

minor discrepancies for the specimen examined. Smirnov & Timms (1983) list this taxon as a synonymy of *Pleuroxus aduncus*. Instead it is quite certainly *Pleuroxus inermis* Sars, 1896.

6. Pleuroxus australis Henry, 1922: 45, pl.7, fig.3. Slide P5893 = HOLOTYPE. Parthenogenetic female without embryos, length 0.45 mm. Body rather low, not expanded dorsally; no keel; suggestions of dimples on shell, but otherwise no markings visible except about 10 curved striae anteriorly; 78 ventral setae on left valve, 75 on right, neither count including any anterior setae; 3 teeth on left valve, 2 on right, broad-based and pointed, deployed along lower posterior margin as in P. aduncus; posterior-dorsal angle weak, posterior-ventral angle strong, emphasised by teeth; eye twice as large as ocellus; IP distance 63 um, PP 187 um, PP/IP ratio 3.0. Postabdomen: mostly obscured by detritus so that shape and relative length of zones not visible; seems elongate; acutely truncate at end, and with only 1 strong denticle here; the couple other more proximal denticles visible are smaller. Postabdominal claw rather stout; longer basal spine much longer than basal width of claw, shorter one less than half as long.

This taxon is not related to any considered in this study. Smirnov & Timms (1983) list it as a synonym of *Pleuroxus similis*, which does not seem correct from the details observable, besides which *P. similis* was described from Chile and hence seems unlikely to be in Australia. At present *P. australis* must be considered a nomen dubium.

7. Chydorus unispinus Henry, 1922: 46, pl.7, figs 4,4a. Slide P5892 = HOLOTYPE. Parthenogenetic female with 2 large eggs, length 0.63 mm. Highly arched dorsally; both posterior-dorsal and posterior-ventral angles reduced by curvature; single, small, slender tooth on either side before posterior-ventral angle; no keel; 8 curved striae anteriorly, continuing posteriorly as a stria closely parallel to ventral margin; no other shell markings; 72 ventral setae on right side, excluding any setae along anterior margin. Eye half again to almost twice as large as ocellus. IP distance 62 µm, PP 171 µm, PP/IP ratio 2.8. Antennules rather short and broad; antennular seta arises about two fifths from end; aesthetasc field surrounded by triangular projections. Postabdomen: anal region equals preanal which is less than postanal; wide, slightly flared out basally; 13 or 14 postanal denticle positions; distal denticles mostly single, proximal ones each with a row of accessory setules. Basal spines on postabdominal claw rather short; longer one about equal to basal width of claw, possibly a little longer; shorter one only about half basal width.

This specimen cannot be associated for certain with any of the taxa considered in this paper. It has a small PP/IP ratio and a small number of ventral setae. The postabdomen and claw resemble those of *Archepleuroxus*, except that there are no chevron-like folds across the distal preanal margin, and the anal portion is not distinctly shorter than the preanal. If this were *Archepleuroxus* it would be from near the bottom of the reproductive size range and hence easily could have just two eggs. The teeth on the shell, though, are not at all like Archepleuroxus. The specimen also resembles *Pleuroxus inermis* in many respects. Except for the prominent shell tooth and the very small number of ventral setae, it resembles the South Australian population of P. inermis, F7961. Henry likened this taxon to Chydorus (= Ephemeroporus) barroisi group because of the slender, backwardly directed tooth at the posterior-ventral angle. However, the large labrum has no teeth, the postabdomen is very different in structure from Ephemeroporus species, and two separated median headpores are readily visible. Smirnov & Timms (1983) consider it a synonym of *Pleuroxus aduncus*, which from the redescription in this paper is obviously incorrect. Chydorus unispinus is a member of the Pleuroxus group of species, but for the moment it must be considered a nomen dubium.

8. Chydorus jugosus Henry, 1922: 46, pl.7, figs 5,5a. Slide P5889 = HOLOTYPE. This is the taxon that initiated this paper. For a while I labelled nearly everything from Australia as *Pleuroxus* cf. *jugosus*, not knowing to which of the many taxa Henry's *jugosus* corresponded. A close study of this specimen, however, did not reveal enough positive characters to make a firm decision, and hence this taxon, at least for the present, must be regarded as a *nomen dubium*. Henry gives the size of the taxon as 0.74 mm, but this specimen measures only 0.56 mm. Comparison with two possibly related taxa from Western Australia - *Plurispina chauliodus* and *Plurispina multituberculata* - puts the specimen near the upper size limit of instar-I, although its morphology, especially of the postabdomen, indicates that it is an instar-II individual.

A single specimen, especially a juvenile, is insufficient to characterise a taxon. The specimen has tubercles on its shell, as do the two species of *Plurispina* from Australia plus *Pleuroxus helvenacus* from New Zealand, but too few details of morphology can be resolved to determine what its affinities are. If it has a greater than normal number of setae in the gnathobasic filter combs of trunklimbs II-V, then it certainly is a member of the genus *Plurispina*. Until more specimens become available, though, the taxon should be left in *Pleuroxus*, which is certainly more appropriate than *Chydorus*. This inadequate holotype of *Pleuroxus jugosus* of Henry is described here in greater detail to help characterise the taxon and to assist in its identification when more individuals become available.

#### Pleuroxus jugosus (Henry)

# Figs 489-493

Chydorus jugosus Henry, 1922: 46, pl.76, figs 5,5a.

*Pleuroxus jugosus.*–Smirnov & Timms, 1983: 22-24, figs 21, 22 (not *Chydorus jugosus* Henry, 1922). [Note: Most of the description and all illustrations in this paper are for *Plurispina chauliodus* n.sp.]

Description of immature holotype female (Figs

489-491). Rostrum of this specimen distorted, bent forward. Eye and ocellus in unnatural positions from contraction of tissues away from headshield; ocellus almost as large as eye. Apparently a keel on head behind pores and on shell; IP distance 45 µm and PP distance 149  $\mu$ m, thus giving a PP/IP ratio of 3.3, which is considerably less than in the tuberculated species that are possibly related. Diagonal ridges and grooves on shell, anterior ones indicated by rows of fine tubercles (Fig.491), posterior ones more prominent, indicated in drawing by dashed lines (Fig.489). Entire head and shell covered by rather coarsely scattered fine tubercles. Colour somewhat darkish, but everything clear in mounted specimen. Posterior margin short, weakly convex; both posterior-dorsal and posterior-ventral angles rounded; no tooth on shell; ventral margin evenly convex. Aesthetascs stop way short of tip of rostrum. Rami of antennae short and stout; terminal spines less than length of terminal segments. Keel of labrum rather short, broadly rounded at tip; posterior angle roughly 90°. Postabdomen with preanal portion shorter than anal portion, which in turn is considerably shorter than postanal portion (Fig.490); about 13 denticles in postanal portion, distal ones being simple, but proximal ones have smaller accessory denticles or setae arranged proximal to them; course of denticles not parallel, distal ones pointing proximally, proximal ones distally, and central ones at right angles; scallops of setae or spinules on lateral surface not visible, nor are crescents of spinules across ventral margin. Postabdominal claw with a marked bend in curvature in concave margin; both basal spines very long and slender, longer than basal width of claw; preanal angle of postabdomen subdued, and postanal angle broadly rounded. Ventral setae on shell 89 on left side and 92 on right side, in both instances excluding any submarginal setae arising anteriorly, which are not visible. Other species have about ten such setae.

Figures 492 and 493 are drawn from the specimen that Smirnov deposited in the AM as *Pleuroxus jugosus* to help bolster the description of the taxon, his number 2805 and the Museum number P27723. Unfortunately, this specimen is from the taxon *Plurispina chauliodus*, which has many distinctive characters as revealed in the species description. The immature holotype is still the only extant specimen of *Pleuroxus jugosus* (Henry, 1922).

**Remarks.** This taxon has fine tubercles on the shell and head, probably a keel, and the preanal portion of the postabdomen is shorter than the anal portion. Moreover, there are about 100 ventral setae on the shell, and the postabdominal denticles extend in different directions rather than being roughly parallel. All these characters apply in varying degrees to the two species of *Plurispina* from Western Australia and to a lesser extent to *Pleuroxus helvenacus* from New Zealand. The elongate body, though, and the short PP distance may be reflections of immaturity rather than being characteristic of adult specimens. The taxon seems 364 Records of the Australian Museum (1991) Vol. 43

related to the two tuberculate species from Western Australia, but counts of the number of spines in the gnathobasic filter combs are needed to determine if it is a member of the genus *Plurispina*.

# Discussion

The high diversity of the chydorid fauna of Australia

was suggested by the paper of Smirnov & Timms (1983). Smirnov in this paper and in his previous papers (Smirnov, 1971, 1977) described five new genera, 14 new species, and two new subspecies of chydorids from Australia. In this paper, considering just the genus *Pleuroxus*, I have described two new genera and five new species. Two of the species – *Pleuroxus inermis* and *Pleuroxus foveatus* – each possibly represents more than one species, but the material available is not adequate to decide. *Pleuroxus hastirostris* and *P. inermis* 



Figs 489-493. *Pleuroxus jugosus* (Henry, 1922) HOLOTYPE, specimen P5589, from AM, immature female: 489. side view; 490. postabdomen; 491. arrangement of denticles into striae in anterior-ventral part of shell. *Plurispina chauliodus* n.sp., specimen P27723, AM, erroneously labelled *Pleuroxus jugosus* by Smirnov & Timms (1983); 492. side view of mature parthenogenetic female; 493. postabdomen.

closely resemble in general characters species of *Pleuroxus* that occur in the Northern Hemisphere. The other six species resemble *Pleuroxus* in many respects, but differ sufficiently so that four of them are removed to new genera, including *Archepleuroxus* established by Smirnov & Timms. The two remaining species are retained in *Pleuroxus*. *Pleuroxus foveatus* might well be placed in a different genus, although its differences from traditional *Pleuroxus* species are not so great as in the others. A decision about *P. helvenacus* cannot be made at the moment, because no gamogenetic individuals are available. Although it has tubercles on the shell and head, it is markedly different from the other two species that share this character and does not belong in the genus established for them.

This fauna was difficult to work with, first because nearly every population studied was suspected initially to be a new species, and second because at first none of the taxa stood out clearly from the others. However, a careful tabulation of the characters found to be important (Table 2) revealed guite clearly the major taxa present. The characters that were most useful in defining the species are: 1) size (length); 2) sizefrequency distribution by instars and stages (Fig.1); 3) number of ventral setae on the shell; 4) surface markings or patterning on the shell and head; 5) presence or absence of a shell tooth and its characteristics; 6) whether the dorsal surface transversely was rounded, ridged or keeled; 7) amount and pattern of pigmentation in intact animals and their ephippia; 8) the PP/IP ratio; 9) nature of the rostrum in males and females; 10) size and feathering of the smaller ODL seta; 11) which of the corm setae is the longest; 12) the number of setae in the gnathobasic filter combs of trunklimbs II-V; 13) number, nature and orientation of the postabdominal denticles; 14) relative length of the preanal, anal and postanal portions of the postabdomen; 15) relative length of the basal spines on the claw; 16) size and shape of the claw of the mature male; 17) whether or not the male seta on the antennule is brush-like; 18) whether the shell flaps are narrowly or broadly attached to the ephippium posteriorly; 19) two or many parthenogenetic eggs per instar, and 20) one or two resting eggs per ephippium.

Other characters used are apparent from the descriptions, but these are more difficult to quantify. Counts of ventral setae were used earlier by Frey (1976) to separate Pleuroxus pigroides from other species of the genus in northern Europe, but this is the first time counts of the setae have been used to help separate members of a group of broadly related species. As mentioned in the species write ups, the number of setae per taxon remains roughly constant over all stages and all instars after instar-I. The number of setae in the gnathobasic filter combs, the relative length of the three portions of the postabdomen, and the PP/IP ratio of mature parthenogenetic females are being used for the first time. Together these characters provide a sensitive means for distinguishing the various species and genera.

There are several points of interest raised by this

material. First, all taxa considered are restricted to Australia or New Zealand. Neither of the two species in New Zealand occurs in Australia. The European species *Pleuroxus aduncus* was claimed to occur in Australia, but it does not. What this suggests is that the chydorid Anomopoda in Australia, as well as various groups of plants and animals that have already been studied, have been isolated from the rest of the world for 60 million years or so, since the time that Australia separated from the last remaining bit of Gondwana. This period of time was sufficient for the differentiation of many new taxa now confined to Australia. The restricted occurrence of these taxa and the fact that, at least for Pleuroxus and related genera, no taxa that have evolved outside of Australia have invaded the continent over this long period, indicate that passive distribution of resting eggs by wind and birds cannot be accomplished as easily as believed by persons who accept the distribution of the chydorids as cosmopolitan. Studies of morphological differences between populations having the same name on different continents have shown the taxa to be different at the species level (see Frey, 1986 for a partial review). Such comparisons have been made between cognate populations in North America, Europe, South-east Asia, Australia, South America, and Sri Lanka. They indicate that one should be cautious about accepting as valid for any chydorid a name originating on some other continent. Only in the Tropics and Subtropics does there seem to be any possibility for conspecific populations to occur naturally on different continents (Rajapaksa & Fernando, 1982, 1987).

Second, the situation in Australia is even more complicated than this, because closely related species can occur in the same region. Australia has had a complicated geological history over the past 60 million years, with at one time the continent being separated into eastern and western portions by the sea. Separation evidently was long enough for many of the isolated populations to differentiate into new species, and there undoubtedly have been other interruptions of formerly continuous ranges. What has become apparent is that many of the taxa in Western Australia seem not to occur in the eastern part of the continent. They are associated with special kinds of aquatic habitats - extremely shallow bedrock pools that dry up completely each summer; waterbodies of varying salinity, chiefly sodium and chloride, to which a number of species of Pleuroxus and related genera have adapted; larger ponds and lakes that tend to be seasonal and in consequence may experience changes in salinity; and others. Such waterbodies in Western Australia and in other arid or semi-arid parts of the continent, have been barely sampled for Cladocera, chiefly by Bayly and Shiel in Western Australia, Timms in Queensland and New South Wales, Williams and Morton in South Australia, Bayly, Morton, and Shiel in Victoria, and Morton, Shiel, and Timms in Tasmania. The high diversity recovered from limited sampling suggests that other species of Pleuroxus and related genera will be revealed by intensive sampling over the year of such special habitats.

Third, there are number of morphological features that are highly distinctive for particular species. For example, the male seta on the antennule of Plurispina chauliodus and Planicirclus alticarinatus is strongly brush-like in the distal segment, whereas other taxa have this structure without lateral setules. Previously the only chydorids known to have a brush-like seta were Saycia cooki (Frey, 1971), and Pleuroxus scopuliferus Ekman, 1900. In addition, the lesser ODL seta varies in size, usually being quite short and with either none or with only a few barely distinguishable setules arising from the distal segment. In the same two species mentioned above, however, the seta is considerably longer and it is strongly brush-like in the distal segment. Most of the chydorids other than species of Eurycercus and Saycia have only a single ephippial egg, but a few species, such as Chydorus ovalis, Chydorus biovatus, and possibly Camptocercus lilljeborgi have two (Fryer & Frey, 1981), and also Chydorus piger (Frey, 1985). Collections of C. biovatus from different lakes in Montana have shown this character to be constant for the taxon, as likewise it is for C. ovalis and probably also C. piger. Thus, the two-egged condition seems unvarying for the taxa that have it. In the present study, two ephippial eggs were found in Archepleuroxus baylyi and in Planicirclus alticarinatus, thereby increasing the known number of species with two ephippial eggs to six. Archepleuroxus is also polyembryonic, the first instance of such a condition in the subfamily Chydorinae. The other instances are the various species in Eurycercus and Saycia in two other subfamilies.

In my initial examination of the populations selected for study I scarcely knew what to call any taxon. Except for Pleuroxus hastirostris and Archepleuroxus baylyi, everything else was labelled Pleuroxus cf. jugosus, a most unsatisfying condition. Not until I began making detailed counts and measurements and arranging the data in tabular form (Table 1) did the various taxa begin to emerge clearly. And in the end, not one of them could be labelled P. jugosus! This is the kind of resolution of taxa that I am confident will be repeated, perhaps may times, in Australia, and no doubt will also occur in other parts of the World when their taxa are studied comparatively and in detail. The number of taxa everywhere, even in Western Europe, is greater than presently accepted in the cosmopolitan mode of thinking about the evolution in this group.

# Summary

The *Pleuroxus* species and related taxa described here show wide morphological variation (summarised in Fig.1 and Table 2). *Pleuroxus hastirostris* is slightly the smallest species, and *Planicirclus alticarinatus* by far the largest. The three populations judged to be *Pleuroxus inermis*, including a population raised from mud by G.O. Sars (1896), are all about equal in size and have much the same population structure, even though the Frey 8026 population from Western Australia is smaller stage by stage and instar by instar than the Frey 7961 population from South Australia. The three populations of Pleuroxus foveatus are somewhat larger than the inermis/hastirostris species. These populations are considered to be the same species, even though there seem to be marked differences in size-structure of instars and stages among the populations. Moreover, nearly all specimens have one more seta in the gnathobasic filter comb of trunklimb III, which suggests possibly a differentiation at the generic level. Archepleuroxus baylyi begins at about the same length at the small end but extends to much larger sizes at the large end. The two species of *Plurispina* from Australia and Pleuroxus helvenacus from New Zealand extend from about 0.5 to about 0.9 mm, and then Planicirclus dwarfs everything else, ranging from 0.75 to 1.75 mm in length. Thus, size distribution alone separates these taxa into at least four and possibly five groups. Although gamogenetic individuals are present in most of the populations studied, unfortunately they are absent from five of them. Hence, the precise characterisation of some of the taxa is difficult to achieve with the present material.

All these taxa except the two species of Plurispina have the curved striae on the anterior part of the shell that are considered characteristic of most Pleuroxus or Pleuroxus-like species. All have the ventral setae on the shell arising from the margin, except for about ten to 15 anteriorly, which arise strongly submarginally along a line that moves inward from the shell margin. In the anterior half of the ventral margin the setae arise from expanded bases, resulting in a weak saw-like configuration. But the number of shell setae varies tremendously, from about 80 in Pleuroxus hastirostris to almost 190 in Planicirclus alticarinatus. The Pleuroxus foveatus populations uniformly have about 100, and the three tuberculate taxa have about 110 to 120 setae. The number of setae per taxon is quite uniform over all instars and stages, being only slightly fewer in instar-I individuals. Except for this one instar, there is no real increase in number during instar ontogeny of either males or females.

Shell markings vary considerably. The small species have smooth shells except for the curved striae in the front. The four populations called *Pleuroxus foveatus* all have small dimples covering the shell. The two species of *Plurispina*, the New Zealand *Pleuroxus helvenacus*, and Henry's single specimens of *Pleuroxus jugosus* are covered with small tubercles at different densities, and in addition they have radiating ridges or folds. *Planicirclus* has the latter to a much greater extent.

The armament at the posterior-ventral corner of the shell is variable. A tooth if present is usually very small, often rounded rather than pointed, and at times easily overlooked. In *Pleuroxus inermis* the specimens from the Sars sample usually had a very small tooth that was difficult to discern because of being oriented along the margin of the shell and not projecting outward. Sars named the taxon *inermis* because it had no tooth, so he thought. The population from South Australia nearly

always had a tooth, whereas the population from Western Australia seldom had one. *Planicirclus* had no tooth on any specimen, and *Archepleuroxus* seldom had a tooth. In contrast, the teeth on *Pleuroxus* aduncus are large, most commonly two in number, and oriented differently than in the Australian taxa.

The small species have the top of the shell rounded from side to side, the others either have a ridge or a keel, with *Planicirclus* having a very sharp and broad keel, which begins on the head immediately behind the pores. The keel on the two species of *Plurispina* likewise begins immediately behind the pores.

The interpore (IP) distance varies only moderately among the taxa, being greatest in *Pleuroxus aduncus*, but the postpore (PP) distance is markedly different, resulting in a PP/IP ratio varying from 2.6 in *Pleuroxus hastirostris* to 12.6 in *Planicirclus*. Aside from *Pleuroxus inermis*, which has a relatively small ratio of three and one half to four, the other taxa range roughly from five to seven.

Typically the species of *Pleuroxus* have 8, 8, 6 and 4 setae in the gnathobasic filter comb of trunklimbs II to V, respectively, but the Plurispina species have 10, 10, 7 and 5, and the Pleuroxus foveatus populations tend to have 8, 9, 6, and 4, the number on limb III in the Shiel 839 population being either 8 or 9 and a few specimens in the Shiel 857 population having 8 instead of 9 setae here. Since the number of these setae is much the same in all species of the subfamily Chydorinae, a marked and consistent difference indicates a different evolutionary line. Pleuroxus helvenacus from New Zealand grossly resembles the two Plurispina species in shape and in having rounded tubercles scattered over the shell, but its gnathobasic setae number 8, 8, 6 and 4. In many respects it seems more closely related to Planicirclus, particularly in the armament of its postabdomen. All the taxa have 7, 7 and 4 feathered setae on the exopodites of trunklimbs III to V, respectively. On trunklimb I the length and nature of the smaller ODL seta varies from taxon to taxon. In most taxa this seta is short and bare, but Plurispina chauliodus and Planicirclus are unique in having this seta strongly brush-like.

The relative lengths of the preanal, anal and postanal portions of the postabdomen are highly variable among the species. Most commonly the preanal and anal portions are about equal in length, but in Pleuroxus helvenacus the preanal portion is shorter than the anal portion, and in Plurispina chauliodus it is much shorter. In Archepleuroxus and Planicirclus the anal region is the shortest of the three. In all species the postanal region is the longest, or else equal in length to the preanal or anal portions. In the large species the ventral margin of the postabdomen flares out markedly basally, and there is a much more extensive lateral armament of rows and crescents of setae. The number and nature of the postabdominal denticles is also variable, ranging from seven to ten in P. aduncus and P. hastirostris to about 20 in Pleuroxus helvenacus and Planicirclus. The denticles also differ as to whether they are single or multiple, most commonly being single distally and multiple proximally.

*Pleuroxus aduncus* and *P. hastirostris* have all the denticles multiple. *Pleuroxus helvenacus* and *Planicirclus* have their distal denticles so close together that they are essentially touching at their bases.

All the males proceed through a three-instar ontogeny, which is apparently characteristic of all species of chydorids. However, there are marked differences in morphology. In *Plurispina chauliodus* and *Planicirclus* the male seta on the antennule is brush-like, whereas all the other taxa have a simple distal segment with no branch setules. Pleuroxus aduncus and Archepleuroxus have the postabdominal claw of the male sigmoid, whereas the other taxa have the claw much as in the female, except possibly being a little shorter and stouter. In Pleuroxus hastirostris there are no postabdominal denticles in the male, just a number of transversely oriented rows or clusters of setae. The shape of the male with reference to that of the females also varies. In many taxa the male is less high relatively than the female, but in *Planicirclus* the males are almost equally round.

polyembryonic, Archepleuroxus is and Archepleuroxus and Planicirclus produce two resting eggs instead of the more traditional one. The amount of pigmentation of the ephippium varies greatly, from being essentially absent in Pleuroxus foveatus to such heavy pigmentation in Plurispina chauliodus and Planicirclus as to obscure all internal details of morphology. Usually the shell flaps that are loosened along the slough line at molting are so broadly connected with the ephippium posteriorly that they almost never are lost completely, but in Pleuroxus foveatus the connection is very narrow, and hence the flaps are usually lost, leaving just the shell tooth and seven to ten ventral setae anterior to it still attached to the ephippium.

Thus, there are many differences between these various taxa and even between different populations of what are considered to be the same taxon. This created difficulties in deciding what the limits of the various species are and whether all these species properly belong to the same genus *Pleuroxus*. All the characters, though, have to be considered in cladoceran systematics, as they are part of the diversification that has developed over time.

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# APPENDIX

Table 1. Pleuroxus and Pleuroxus-like taxa claimed to occur in Australia or New Zealand. Pleuroxus laevis, P. denticulatus, and P. similis described from other continents are probably absent. Pleuroxus aduncus from Europe is definitely absent, even though Smirnov & Timms (1983) synonymised Chydorus denticulatus, Chydorus unispinus and Alonella nasuta with it. They also synonymised Pleuroxus australis with P. similis. Pleuroxus jugosus cannot be defined from the single immature female available. The taxa that are numbered are the ones considered in detail in this paper. The paper by Smirnov (1989) describing two species of Pleuroxus was published after this paper had been accepted. Pleuroxus triocellatus is similar in general style to species 5 to 9 but differs from them in important characters.

	Taxon	Described from	Comments
1.	Pleuroxus aduncus (Jurine, 1820) Pleuroxus laevis Sars, 1861 Pleuroxus denticulatus Birge, 1879	France Norway Wisconsin	Absent from Australia and New Zealand Probably absent Probably absent
2.	Pleuroxus inermis Sars, 1896 Pleuroxus similis Vavra, 1900	New South Wales Chile	Widespread and common in southern Australia Probably absent
3.	Pleuroxus hastirostris Sars, 1903 Alonella nasuta Smith, 1909	New Zealand Tasmania	Only in New Zealand Seems likely in <i>Pleuroxus</i> group but species uncertain. Synonym of <i>P. aduncus</i> in Smirnov & Timms (1983)
	Chydorus denticulatus Henry, 1918 Pleuroxus reticulatus Henry, 1918	New South Wales New South Wales	Synonym of <i>P. aduncus</i> in Smirnov & Timms (1983) From type specimen of 1918 and illustrations in Henry (1922), Smirnov (1977) decided this was <i>Monope reticulata</i> (Henry, 1922) even though illustrations in Henry (1918) are of a species of <i>Alonella</i> .
	Chydorus unispinus Henry, 1922 Chydorus jugosus Henry, 1922 Pleuroxus australis Henry, 1922	NewSouthWalesNewSouthWalesNewSouthWales	Synonym of <i>P. aduncus</i> in Smirnov & Timms (1983) Identity unknown; only immature female available Synonym of <i>P. similis</i> in Smirnov & Timms (1983)
4.	Archepleuroxus baylyi Smirnov & Timms, 1983 Pleuroxus triocellatus Smirnov, 1989 Pleuroxus kakaduensis Smirnov, 1989	Western Australia Western Australia Northern Territory	Known from Victoria, Tasmania and Western Australia Apparently different from any species in this table. Not related to <i>P. aduncus</i> .
5.	Pleuroxus foveatus n.sp.	Western Australia	
6.	Plurispina chauliodus n.gen., n.sp.	Western Australia	
7.	Plurispina multituberculata n.sp.	Western Australia	
8.	Pleuroxus helvenacus n.sp.	New Zealand	Restricted to New Zealand?
9.	Planicirclus alticarinatus n.gen., n.sp.	Western Australia	

San no.	mple Taxon		Region	Sample	Total no.	Length mature females Range (no.)	Surface pattern	Top of shell	<u>Vent</u> Mean	t <u>ral setae</u> Range (no.)	shell teeth	<u>IP dist</u> Mean	<u>tance (μm)</u> Range (no.)	PP/IP ratio
1.	Pleuroxus ad	duncus	Denmark	Frey 3004	72	0.48-0.60(39)	smooth	rounded	84	79-87(19)	2(0-3), strong	67	63-72(6)	3.0
2. 2a 2b.	Pleuroxus in	iermis	NSW WA SA	Sars F413 Frey 8026 Frey 7961	9 199 221 235	0.44-0.60(190) 0.45-0.57(49) 0.47-0.63(107)	smooth smooth smooth	rounded rounded rounded	88 90 89	84-93(6) 84-97(19) 82-96(15)	1(0-1), very small 0(0-1) 1(0-1)	53 53 59	47-58(3) 49-58(13) 56-63(12)	3.8 4.0 3.5
3.	Pleuroxus h	astirostris	NZ	Frey 8388	235	0.40-0.50(61)	smooth	rounded	78	74-81(8)	1 sharply pointed	56	54-59(6)	2.6
4. 4a. 4b. 4c.	Pleuroxus fo	oveatus	WA WA WA WA	Shiel 856 Shiel 857 Bayly 51 Shiel 839	16 283 35 107	0.57-0.65(2) 0.51-0.71(63) 0.53-0.69(21) 0.49-0.65(67)	dimpled dimpled dimpled dimpled	weak ridge weak ridge weak ridge weak ridge	101 102 100 102	93-106(18) 94-108(17) 89-107(12) 100-113(6)	1(0-1)	46 47 53 55	45-47(3) 43-50(9) 52-54(5) 50-59(7)	6.4 6.2 5.8 4.7
5.	Archeoleurox	cus baylyi	Tas.	Morton 35	128	0.61-0.95(40)	smooth	rounded	91	84-102(12)	0(0-1)	62	59-63(3)	4.7
6. 6a. 6b.	Plurispina ch	hauliodus	WA WA WA	Bayly 31 Bayly 58 Bayly 84	83 59 25	0.68-0.83(15) 0.68-0.85(30) 0.77-0.90(13)	tubercles and ridges	keel	107	100-113(17)	1, triangular	42	34-47(11)	7.6
7.	Plurispina m	ultituberculata	WA	Bayly 66	98	0.73-0.88(17)	tubercles and sloping ridges	keel	122	116-127(6)	1(1-2), triangular	54	52-59(6)	6.8
8.	Pleuroxus h	elvenacus	NZ	Frey 8374	36	0.52-0.89(36)	tubercles and radiating ridges	ridge	118	108-126(19)	1(0-2)	56	47-61(6)	5.4
9.	Planicirclus	alticarinatus	WA	Shiel 792	111	1.21-1.75(43)	many ridges	strong keel	186	167-203(20)	0	60	47-72(10)	12.6

Table 2. Characters of importance in separating the various species and genera.

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Table 2 (cont'd). Characters of importance in separating the various species and genera.

Sample No.	2nd seta on ODL of TL I brushy?	G fi II	natho lter III	obas setae IV	ic e V V	Relative length of regions of postabdomen	Postabdominal denticles	Male seta on antennule brushy?	Male characters	Other characters
1.	no	8	8	6	4	preanal=anal <postanal< td=""><td>7-10, all multiple</td><td>no</td><td>p.a. tapered; claw sigmoid</td><td></td></postanal<>	7-10, all multiple	no	p.a. tapered; claw sigmoid	
2. 2a. 2b.	no no no	8 8 8	8 8 8	6 6 6	4 4 4	preanal=anal <postanal< td=""><td>12-13, long</td><td>no</td><td></td><td></td></postanal<>	12-13, long	no		
3.	slightly	8	8	6	4	preanal=anal <postanal< td=""><td>8-10, all multiple</td><td>no</td><td>no denticles on p.a.; 9 rows of setae</td><td></td></postanal<>	8-10, all multiple	no	no denticles on p.a.; 9 rows of setae	
4. 4a 4b 4c	no	8 8 8 8	9 9(8) 9 8(9)	6 ) 6 6 ) 6	4 4 4 4	preanal=anal <postanal< td=""><td>13-15, long</td><td>no</td><td></td><td>ephippial shell flaps easily lost</td></postanal<>	13-15, long	no		ephippial shell flaps easily lost
5	no	8	8	6	4	anal <preanal=postanal< td=""><td>12</td><td>no</td><td>claw short, somewhat sigmoid</td><td>2 ephip. eggs; polyembryonic</td></preanal=postanal<>	12	no	claw short, somewhat sigmoid	2 ephip. eggs; polyembryonic
6. 6a. 6b.	yes	10	10	7	5	preanal< <anal=postanal< td=""><td>12-15</td><td>yes</td><td>2 strong denticles on rostrum</td><td>claw; spines short, setae long</td></anal=postanal<>	12-15	yes	2 strong denticles on rostrum	claw; spines short, setae long
7.	no or weakly	10	10	7	5	preanal=anal <postanal< td=""><td>12-15, in different directions</td><td>_</td><td></td><td>claw; spines short, setae long; tubercles densely packed</td></postanal<>	12-15, in different directions	_		claw; spines short, setae long; tubercles densely packed
8.	no	8	8	6	4	preanal <anal<postanal< td=""><td>20, almost touchin at bases distally</td><td>.g –</td><td></td><td>p.a. flared outward basally</td></anal<postanal<>	20, almost touchin at bases distally	.g –		p.a. flared outward basally
9.	strongly	8	8	6	4	anal <preanal=postanal< td=""><td>20, very long</td><td>yes</td><td>tubercle at tip of rostrum</td><td>middle and posterior corm setae almost equal; 2 resting eggs; heavy pigmentation in ephip. female</td></preanal=postanal<>	20, very long	yes	tubercle at tip of rostrum	middle and posterior corm setae almost equal; 2 resting eggs; heavy pigmentation in ephip. female

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Table 3. Morphological differences between Pleuroxus aduncus sensu stricto from Europe and Pleuroxus inermis from Australia.

Characters	P. aduncus	P. inermis
MATURE FEMALE		
Shape	<ol> <li>less high</li> <li>dorsal margin concave near posterior- dorsal angle</li> </ol>	<ol> <li>relatively higher</li> <li>dorsal margin evenly rounded, without concavity</li> </ol>
Shell	<ol> <li>0-4 large denticles at posterior-ventral angle, most commonly 2</li> <li>ventral setae 84 (range 79-89, n=19)</li> <li>submarginal setules along posterior margin short, relatively few, and widely spaced</li> </ol>	<ol> <li>0-1 very small denticle at posterior-ventral angle, usually 0 in Western Australia population</li> <li>ventral setae 89 (range 82-97, n=40)</li> <li>posterior submarginal setules rather long, numerous, closely spaced</li> </ol>
Head	<ul> <li>6. IP distance 67 μm (range 63-72, n=5)</li> <li>7. PP/IP ratio 3.0</li> </ul>	<ol> <li>IP distance 53-59 μm (range 47-63, n=28)</li> <li>PP/IP ratio 3.5-4.0</li> </ol>
Antenna	<ol> <li>8. 1 terminal seta on antennal endopodite much shorter than other 2</li> <li>9. no spine on basal segment of exopodite</li> </ol>	<ol> <li>8. 1 terminal seta on antennal endopodite only slightly shorter than other 2</li> <li>9. small spine on basal segment of exopodite</li> </ol>
Labrum	10. keel quite broad; tip not strongly attennuated	10. keel narrower and tip finer
Trunklimb I	11. second spine on ODL extremely small	11. second spine on ODL longer, quite conspicuous
Postabdomen	<ul><li>12. 7-10 marginal denticle positions</li><li>13. all denticles multiple</li><li>14. only a short distal portion of preanal margin not double</li><li>15 abdominal setae long reaching middle of</li></ul>	<ul> <li>12. about 12-13 marginal denticle positions</li> <li>13. distal denticles single; only proximal ones multiple</li> <li>14. longer portion not double</li> <li>15 abdominal setae shorter not reaching to one</li> </ul>
MATURE MALE	anal groove or beyond	third of anal groove
Dostabdomon	16 strongly tangend distally to have of along	16 weakly taparad as in famale, not narrowed to
rostabuomen	To strongly tapered distanty to base of claws	base of claws
	17. about 7 oblique rows of spinules (or denticles) in postanal region	17. about 13 denticles or denticle positions, only a few of proximal ones multiple and weakly oblique, those in distal half nearly all single
Postabdominal claws	18. distinctly sigmoid; longer basal spine irregular	18. claw and longer basal spine both evenly curved

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