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Taxonomic revision

A revision of Australian river prawns, *Macrobrachium* (Crustacea: Decapoda: Palaemonidae)

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Abstract

A taxonomic revision of Australian *Macrobrachium* identified three species new to the Australian fauna – two undescribed species and one new record, viz. *M. auratum* sp. nov., *M. koombooloomba* sp. nov., and *M. mammillodactylus* (Thallwitz, 1892). Eight taxa previously described by Riek (1951) are recognised as new junior subjective synonyms, viz. *M. adscitum adscitum*, *M. atactum atactum*, *M. atactum ischnomorphum*, *M. atactum sobrinum*, *M. australiense crassum*, *M. australiense cristatum*, *M. australiense eupharum* of *M. australiense* Holthuis, 1950, and *M. glypticum* of *M. handschini* Roux, 1933. Apart from an erroneous type locality for a junior subjective synonym, there were no records to confirm the presence of *M. australe* (Guérin-Méneville, 1838) on the Australian continent. In total, 13 species of *Macrobrachium* are recorded from the Australian continent. Keys to male developmental stages and Australian species are provided. A revised diagnosis is given for the genus. A list of 31 atypical species which do not appear to be based on fully developed males or which require re-evaluation of their generic status is provided. Terminology applied to spines and setae is revised.

Introduction

River prawns of the genus *Macrobrachium* are a conspicuous and important component of freshwater and estuarine ecosystems throughout tropical and warm temperate areas of the world. Although members of the genus are also commonly referred to as 'freshwater' prawns, some are entirely restricted to estuaries and many require marine influence during larval development.

Most members of the genus are easily recognisable by the well developed, often elongated second chelipeds, which in the males of many species may exceed the body length. Approximately 210 species of *Macrobrachium* are presently recognised, with nearly half of these described in the 50 or so years since the last major revisionary works on the group (Holthuis, 1950, 1952a). Typically, *Macrobrachium* are epigeal, epibenthic and largely nocturnal, although several hypogeal cave species have also been described. Unlike most related palaemonine genera, members of the genus typically have well-developed agonistic behaviour and a solitary lifestyle.

Many species grow to a sufficient size to be used for human consumption. Holthuis (1980) listed 49 species of interest to fisheries throughout the world. The Giant River Prawn, *M. rosenbergii*, has been farmed commercially both within and outside its natural range in localities such as Asia, Hawaii, the Americas, and New Zealand.

From a taxonomic point of view, the genus is one of the more challenging decapod crustacean groups (Holthuis, 1950, 1952a; Chace & Bruce, 1993). The two main morphological features which have traditionally provided characters for separating species, the rostrum and the second pereiopods, are often highly variable within species (Holthuis, 1950). The second pereiopods in particular show a very high level of developmental and sexual variation, including allometric growth in males.

Another major factor contributing to the difficulty of working on the genus is the influence of social dominance on male morphology. In the past it has often been assumed that all sexually mature, fully grown males have developed second pereiopods. However, the importance of behavioural dominance in the morphology of male *M. rosenbergii* was demonstrated by Kuris et al. (1987). Secondary sexual characters such as the form of the second pereiopods are most developed in dominant males and their development is not strictly dependent on size and age. Although fully developed dominant males are usually among the largest individuals, a significant percentage of large subordinate males with undeveloped or developing second pereiopods may be present at any given locality. This is particularly the case where food resources are limited e.g. a drying lagoon on an episodic watercourse. The problem of correctly distinguishing fully developed males when describing new species was well illustrated by the taxonomy of the Australian fauna prior to this study. A number of nominal Australian taxa appeared to have been based on large subordinate males without fully developed chelipeds.

Taxonomic records of *Macrobrachium* from Australia date back to the early carcinological literature. The first record was by Olivier (1811) who reported *Palaemon ornatus* (= *Macrobrachium lar*). Over the next 140 years the Australian fauna received little attention, apart from several single species descriptions, new records and synonyms (Heller, 1865; Ortmann, 1891; De Man, 1908; Roux, 1933; Holthuis, 1950). The first revisionary study of the Australian fauna was by Riek (1951). Riek's study increased the number of known species from six (Holthuis, 1950) to ten. He also described six new subspecies.

Lee (1979) re-evaluated Riek's subspecies of *M. australiense* using morphological characters and a study of F_1 progeny reared in the laboratory and concluded that the differences found 'do not appear to be sufficiently large or consistent enough to warrant dividing the species into 4 sub-species'.

Fincham (1987) described a new species, *M. bullatum*, from Magela Ck and the Alligator Rivers region, N.T. He also provided a key to Australian species based largely on the key of Riek (1951). However, he also questioned the validity of Riek's subspecies of *M. australiense*, 'the morphological characters separating many of Riek's subspecies were small and often involved length ratios of pereiopod segments, which may change during development'. Furthermore, Fincham noted that the holotype of *M. tolmerum* Riek was a non-ovigerous female rather than a male.

In addition to recognised problems with the Riek's classification, some of the material in the Queensland Museum collection appeared outside the range of variation recorded for Australian species. This material appeared to represent three new Australian records, viz., *M. equidens* (Dana, 1852), *M. idae* (Heller, 1862a, b) and *M. mammillodactylus* (Thallwitz, 1892), and two undescribed species. The first two of the new records, *M. equidens* and *M. idae*, have been published elsewhere (Bruce & Coombes, 1997; Short, 2000) whereas the third is reported in this paper.

One of the undescribed species was first recognised by Kneipp (1979) in an unpublished Ph.D. thesis. This species was also well represented in the QM collection through field expeditions to northeast Queensland during the last decade. The other new species was originally collected by Dr S. Bunn and Mr M. Bray (Griffith University) during a limnological study for the proposed Tully-Millstream hydroelectric scheme in 1990. A Queensland Museum expedition to the upper Tully River area in November 1992 yielded detailed habitat data and a good representative range of specimens including the first fully developed males.

Methods and materials

A taxonomic revision of Australian *Macrobrachium* was undertaken using external morphological characters supplemented with biological

and ecological data. The study area was limited to the Australian continent and associated continental islands. External Australian territories such as Christmas Island were not investigated. Extensive collections of preserved material housed in the Queensland Museum, Northern Territory Museum of Arts and Sciences, Australian Museum, Museum of Victoria and South Australian Museum were studied. A field collecting program in Queensland and the Northern Territory provided additional distributional records and new information on behaviour, habitat ecology, and live colouration. In total over 5000 specimens and 1000 registered museum lots were examined.

Abbreviations used: AM, Australian Museum; Ck/s, creek, creeks; CL, postrostral carapace length in mm measured from orbital margin to dorsolateral invagination of posterior margin; CSIRO, Commonwealth Scientific and Industrial Organisation; CYPLUS, Cape York Peninsula Land Utilisation Study; diam., diameter; ERISS, Environmental Research Institute of the Supervising Scientist; hmstd, homestead; FAO, Food and Agriculture Organization of the United Nations; Hds, heads (as in river heads at the junction with the sea); Hwy, highway; imm., immature; MNHN, Muséum Nationale d'Histoire Naturelle, Paris; Mt/s, Mount, Mountains; *n*, number of measurements recorded; NMV, National Museum of Victoria (now Museum of Victoria); NNM, National Natural History Museum, Leiden; N.P., National Park; N.T., the Northern Territory; NTM, Northern Territory Museum of Arts and Sciences; ovig., ovigerous; P, pereiopod; PL, pleopod; ppm, parts per million; ppt, parts per thousand; QDPI (Fisheries), Queensland Department of Primary Industries, Fisheries and Land Utilisation; Qld, Queensland; QM, Queensland Museum; R., river; Ra., mountain range; Rd, road; SAM, South Australian Museum; S.F., state forest; Stn, pastoral station; T, thoracic sternite; TL, total length in mm measured from tip of rostrum to tip of telson; U.S.A., United States of America; W.A., Western Australia; WAM, Western Australian Museum.

Characters

An initial morphological character list was compiled using the DELTA system (discussed below) from descriptions, diagnoses, keys, notes and illustrations of *Macrobrachium* in the literature. This was refined and expanded after a detailed examination of the *Macrobrachium* collection in the Queensland Museum and non-Australian *Macrobrachium* in several major European museums. A schematic drawing of a generalised *Macrobrachium* showing the main morphological features is illustrated in Figure 1.

Biological characters, such as habitat, life history, and behavioural traits were also compiled from the literature. These were expanded and refined during field expeditions in northern Australia.

Delimitation of species

Species were delimited using unique character states or character state combinations. In the case of well-established taxa, previous diagnoses and known limits of variation were also used. Reproductive isolation was inferred from the degree of morphological difference and life history traits.

Descriptions and diagnoses

Species accounts are presented in approximate phylogenetic order based on preliminary phylogenetic analyses. The descriptions of the two new species are based primarily on the fully developed males designated as holotypes. Significant infraspecific variation among the remaining type material is included within parentheses where applicable.

Diagnoses of previously described species are based on material examined first hand and accounts in the literature. Synonymies are complete unless stated otherwise. Non-ovigerous females are simply listed as 'females' in the material examined. Developed ova are recognised by the presence of eye spots. The term 'cheliped' or 'second cheliped' refers to pereiopod 2 (P2) unless explicitly referred to as pereiopod 1 or first cheliped. Measurements were made with vernier callipers (with or without the aid of a stereo microscope) and using a stereo microscope and stage micrometer.

Collection lots in the material examined for each species are ordered first by drainage division and then within drainage divisions by drainage basin in a clockwise direction around

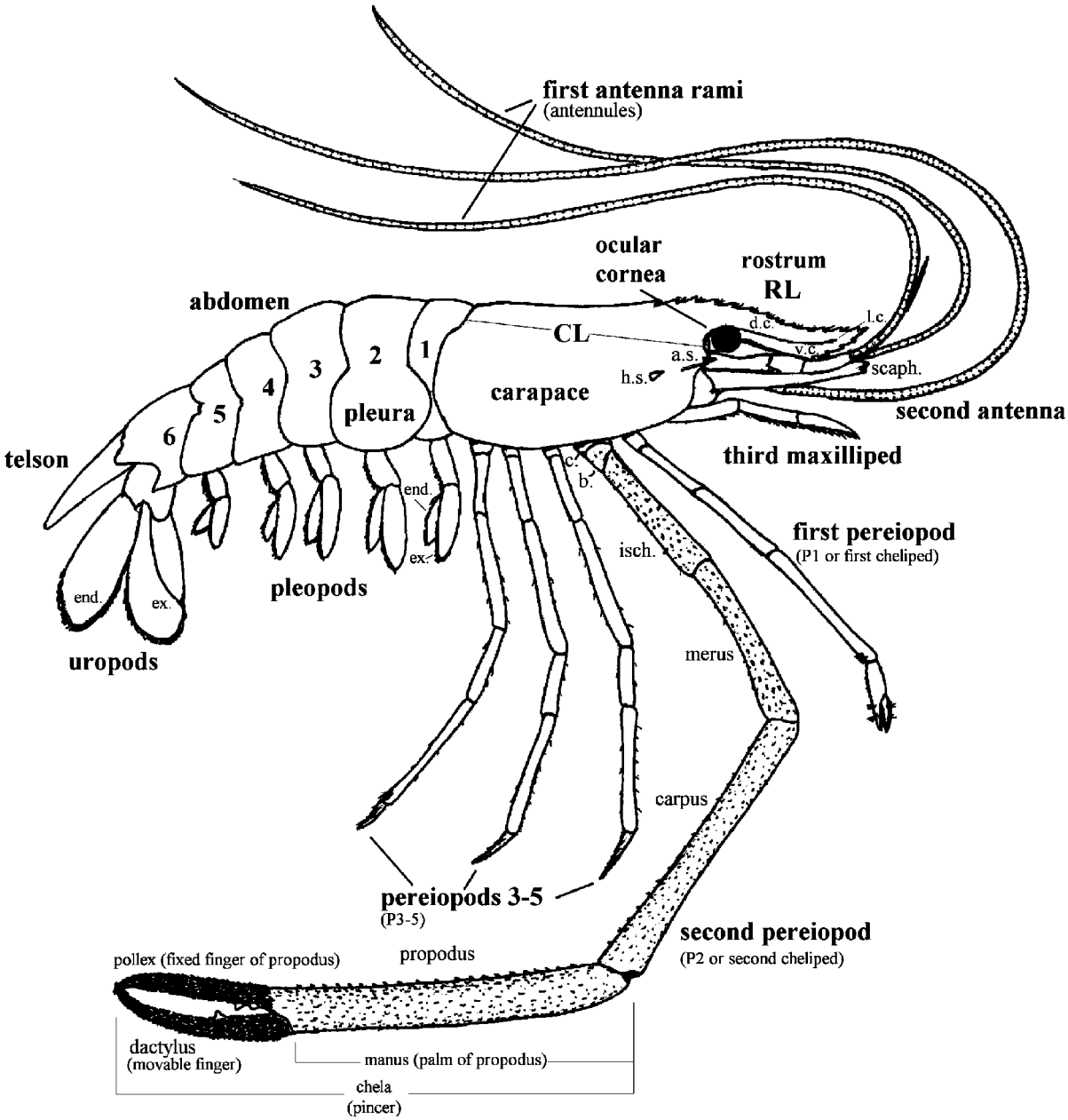

Figure 1. Schematic drawing of a generalised *Macrobrachium* in lateral view (right appendages only). Abbreviations: a.s., antennal spine; b., basis; h.s., hepatic spine; c., coxa; CL, carapace length; d.c., dorsal carina (of rostrum); end., endopod; ex., exopod; isch., ischium; l.c., lateral carina (of rostrum).

Australia (endorheic drainage divisions are presented last). Drainage divisions follow those of Allen (1989) except for the Northwestern and Gulf of Carpentaria Divisions which were combined into a single 'Northern' Division in this study.

Within the major drainage divisions, drainage basins follow the system of the Australian Water Resources Council (1976) except for endorheic basins within the major inland drainage divisions which have not been differentiated e.g. Murrumbidgee River and Darling River within the Mur-

ray-Darling division. The drainage scheme used in this study is presented in Figure 2.

Full collection data are given for the two new species and the new Australian record, including latitudes and longitudes. For the remaining species, only museum catalogue numbers and collection localities are given. If required, full collection data for these species are available upon request from the author.

Line art and photography

Drawings were made with the aid of a camera lucida on a Wild M-5 stereo microscope or Olympus BH-2 compound microscope. These original drawings were then inked and scanned at 600 d.p.i. (dots per inch) as 2 bit 'line art' using a HP DeskScan 2100C scanner. Scanned images were saved as compressed '.tif' files and composed, tidied and labelled in Micrografx Picture Publisher versions 5.0 and 8.0. Final figures were saved in native Picture Publisher format ('.pp5' or '.ppf' files) and printed on a 600 d.p.i. HP LaserJet printer.

Photographs were taken with a SLR 35 mm camera using either black and white film or colour transparency film. Where necessary photographic images were scanned onto Kodak PhotoCD and electronically edited to remove distracting background shadows etc.

The DELTA system

This software package was developed by the CSIRO Division of Entomology and provides a method for encoding taxonomic descriptions for computer processing. The DELTA (DEscriptive Language for TAxonomists) system includes a set of DOS programs (regularly updated) for producing and typesetting natural-language descriptions and keys, for interactive identification and information retrieval (INTKEY), and for conversion of the data to formats required for phylogenetic and phenetic analysis (Dallwitz et al., 1995).

The versions of DELTA (up to edition 4.02) used during this study were only available as non-graphical (with the exception of the interactive key program, INTKEY 4.0, which ran as a Windows program) DOS-based directive and program files.

Collecting methods

Several methods were used to capture live material. Scoop netting along the banks of watercourses among vegetation and fallen timber is a reliable method for capturing juveniles, young adults and ovigerous females – large non-ovigerous adults usually evade the net unless water levels are low and suitable shelter limited. When water levels are low (usually at the end of winter in northern Australia) a broad triangular net (approx. 60 cm wide) gripped at the sides and thrust rapidly through leaf litter beds can be highly productive. Another productive technique requires two people – a broad net is held by the first person against a bank immediately below rocks and organic debris, the second person rapidly turns over rocks and scoops debris in the direction of the net, the first person then scoops rapidly through the area. In shallow rocky riffle areas some species can be easily collected by utilising the current – a flat bottomed scoop net is held immediately down current of a rock and scooped up current as the rock is turned over.

Most of the large adults captured during this study were collected using baited traps set overnight in areas with suitable cover (generally along the banks of creeks and rivers among tree roots, fallen timber or large rocks) in 1–2 m of water. The most practical traps to use are collapsible bait fish traps. These can be easily transported in a back pack or rectangular plastic bucket. In estuarine areas, where mud crabs (*Scylla serrata*) are likely to be common, durable wire mesh traps are more practical to use.

Many different types of baits were trialed. Baits containing a high percentage of animal fat were found to be the most effective. On long expeditions in remote areas, dry dog pellets were the most convenient to use. When immersed these pellets soften and expand but leach slowly into the surrounding water. After removal from the water the pellets again dry out and can be re-used many times. Barbecued chicken is also an excellent bait.

Electrofishing is by far the most efficient technique for capturing large males. It is particularly effective for *Macrobrachium lar*, which was not easily captured using baited traps. The most productive electrofishing technique is to use short bursts of current with the electrode net held near

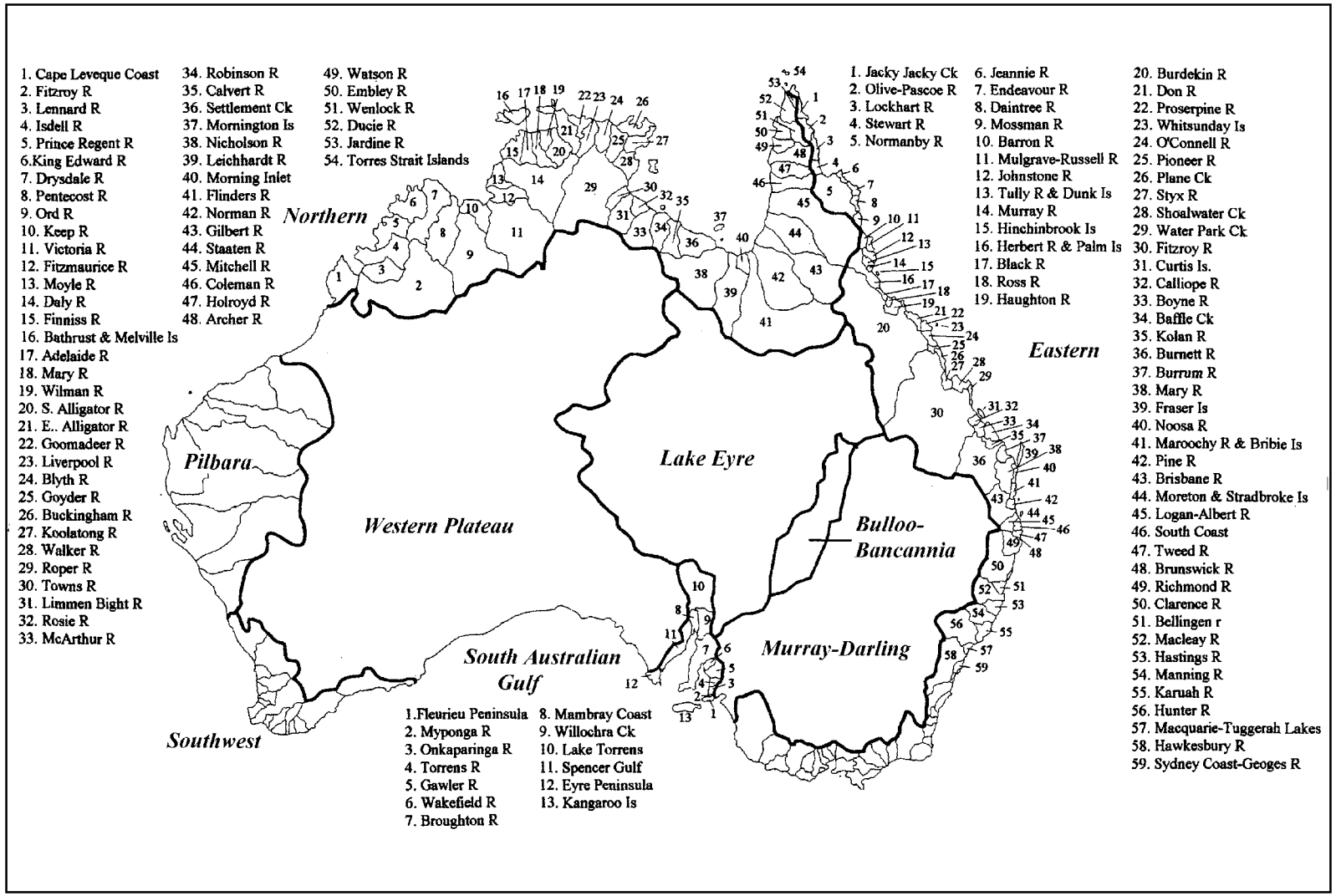

Figure 2. Drainage divisions (italicised) and exorheic basins (those where *Macrobrachium* have been recorded are numbered) used in study (modified from Australian Water Resources Council, 1976).

suitable hiding places. Large males with well-developed chelipeds need to be handled carefully after being shocked. It is advisable not to handle specimens while the muscles are still contracting to avoid loss of the second chelipeds. If a 'shocked' prawn is not handled until it starts to move naturally, damage is minimised.

Habitat ecology

Physico-chemical habitat data were obtained at over 100 collecting sites in Queensland and the Northern Territory. Equipment included a TPS LC82 dissolved oxygen meter (DO_2 and temperature), mercury thermometer (temperature), refractometer (salinity), Hach model 17-N wide range indicator pH test kit or Merck Universalindikator pH 0–14 paper (pH), and Hach model 5-EP total hardness (20–400 mg/l) test kit or Aquasonic water hardness test kit (total hardness). Altitudes were estimated from the Australia 1:100 000 topographic survey map series R631. Classification of rainforest types follows Webb & Tracey (1981).

Distribution maps

Localities for museum records were stored in a relational database (Rbase versions 4.5++ for DOS and 6.1 for Windows) as latitudes and longitudes and then imported into MapInfo as point files. Each species was then mapped onto an Australian base map in MapInfo.

Results

Characters

Many potential morphological characters were evaluated during this study. A large percentage of these were found to be of limited usefulness. Some characters were initially promising but turned out to be impractical to use. For example, the presence of clumps of short heavily tanned setae along the edge of one or more cusps on the crown of each molar process seemed to show good differences between species (as noted by Fujino & Miyake (1968) for species of *Palaemon*) but were often abraded off in older specimens.

The great majority of useful characters were similar to those used by previous workers, e.g. rostral, antennular, scaphocerite, ocular, pereiopod, pleopod, telson and uropodal features. Some traditional taxonomic characters, although apparently useful in other regions of the world, were of limited value for the Australian fauna. Generally these were found to be too variable (showed marked variation between individuals of a similar size and sex or a large degree of developmental variation) or showed little interspecific variation among Australian taxa. Some of the morphological characters that were evaluated and eventually abandoned include:

Anterior mouthparts: Apart from the mandibular incisor processes and third maxilliped, most mouth appendages were found to be highly conservative in the genus and of little value for separating species.

Pereiopod 1: The relative length and shape of the segments of P1 was largely uninformative among Australian species.

Posteroventral abdominal pleura: The shape of the abdominal pleura showed considerable variation and were not consistent enough to use for distinguishing Australian species.

Fifth and sixth abdominal segment lengths: The relative lengths of the fifth and sixth abdominal segments were found to be uninformative for Australian species.

Some structures were not used because they were often damaged in adult specimens. A good example is the shape of the posterior margin of the telson. Large adults often have a damaged posterior telson and as a result tend to have a much blunter margin than young specimens.

In general, proportional characters such as length breadth ratios of appendage segments were largely uninformative and at best useful for grouping similar taxa together. Typically, proportional characters displayed a high degree of developmental variation (particularly among males). The range of values for these characters generally showed a high degree of overlap between closely allied taxa. Historically, exact measurements have also been given for the relative lengths of second pereiopod segments in relation to one another. Such precise measurements are of limited value unless a range is given for a good series of specimens representing a specific stage of

development (e.g. fully developed males). In this study, relative segment lengths were described for fully developed males and given as approximate values only e.g. carpus about equal in length to chela.

The precise shape of cuticular processes was also found to be of little use in Australian taxa. Median processes on the thoracic sternites often varied from strongly spinate to rounded, even between individuals of a similar size. Hence these were simply described as 'median process present' or 'median process absent'.

Although many of the characters evaluated proved to be of limited usefulness, there were still a number of highly useful taxonomic characters discovered during the process. Some of these are very important in that they show limited sexual and developmental variation, a rarity for the genus. The new characters are as follows:

Inferior orbit shape: Short and Marquet (1998) discussed the shape of the inferior orbit in New Caledonian *Macrobrachium*. In some species, e.g. *M. australiense*, this is a variable character, but in most it is highly consistent between sexes and specimens of different ages. Most species have the inferior orbit moderately produced. The shape of the inferior orbit may be either angular with the postantennular carapace margin concave or straight, or obtuse with the postantennular carapace margin convex and evenly rounded (Fig. 3A–C). The shape of the inferior orbit is also a good character to use in keys.

Bec Ocellaire: This structure is an upwardly directed beak-like structure located on the ophthalmic somite between the eyestalks (Fig. 4A). When well developed, the upper bec ocellaire almost rests against the ventral carina of the rostrum. The bec ocellaire has been rarely used in *Macrobrachium* descriptions. The majority of *Macrobrachium* have a well-developed bec ocellaire but in some species it is poorly developed or absent e.g. *M. placidulum* (De Man, 1892).

Epistome: The epistome is often used in descriptions of reptant decapods, but has rarely been used for carideans. In *Macrobrachium* and other carideans the epistome is usually obscured by the mouthparts whereas in reptant decapods the structure is immediately visible. In many *Macrobrachium* the epistome is divided into two anteriorly rounded lobes (Fig. 4C). These species are hard to separate using the epistome. In other *Macrobrachium* the structure shows more variation, e.g. lobes carinate obliquely (Fig. 12C) or longitudinally (Fig. 16B), lobes produced anteriorly (Fig. 29B) or lobes produced ventrally as horns. The epistome is a useful identification character for these species. Epistome features are generally more clearly developed in large adults.

Thoracic sternite: Like the epistome, the thoracic sternum is rarely described in carideans but commonly used in descriptions of reptant decapods. Again, the sternum is more easily viewed in reptant decapods than carideans. Most of the sternal segments show insignificant variation in *Macrobrachium* but sternites 4 (between first pereiopods) and 8 (between fifth pereiopods) are useful. Sternite 4 generally is armed with a well-developed median process (Fig. 3D). In some species the process is greatly reduced or absent. This is consistent between sexes and at different stages of development. Some variation is shown in the shape of the process, i.e. may vary from rounded to spinate in the same species. However, the presence or absence of a median process is very consistent between sexes and individuals at different stages of development. When absent it is a useful key character.

Developed males in some species also have a median process posteriorly on sternite 8. When present, the process is generally blunt in old developed males but more spinate in young males. The development of the anterolateral lobes on sternite 8 also varies between species. These lobes are either well separated (Fig. 3E), narrowly separated or contiguous postero-medially in developed males.

Pre-anal carina on inter-uropodal sclerite: The presence or absence of a pre-anal spine is a commonly used character in atyid shrimps. In the same position there is often a well-developed pre-anal carina in many species of *Macrobrachium* (Fig. 4B). Again this is a highly consistent non-sexual character which is particularly useful for keys.

During this study I was unable to find an anatomical term for the segment on which the pre-anal carina is located. As this segment does not appear to be on any of the main abdominal somites and occurs ventrally between the uropods I have termed it the inter-uropodal sclerite (Short & Marquet, 1998). Pereira (1997) termed the same segment the anal plate although the anus is located immediately

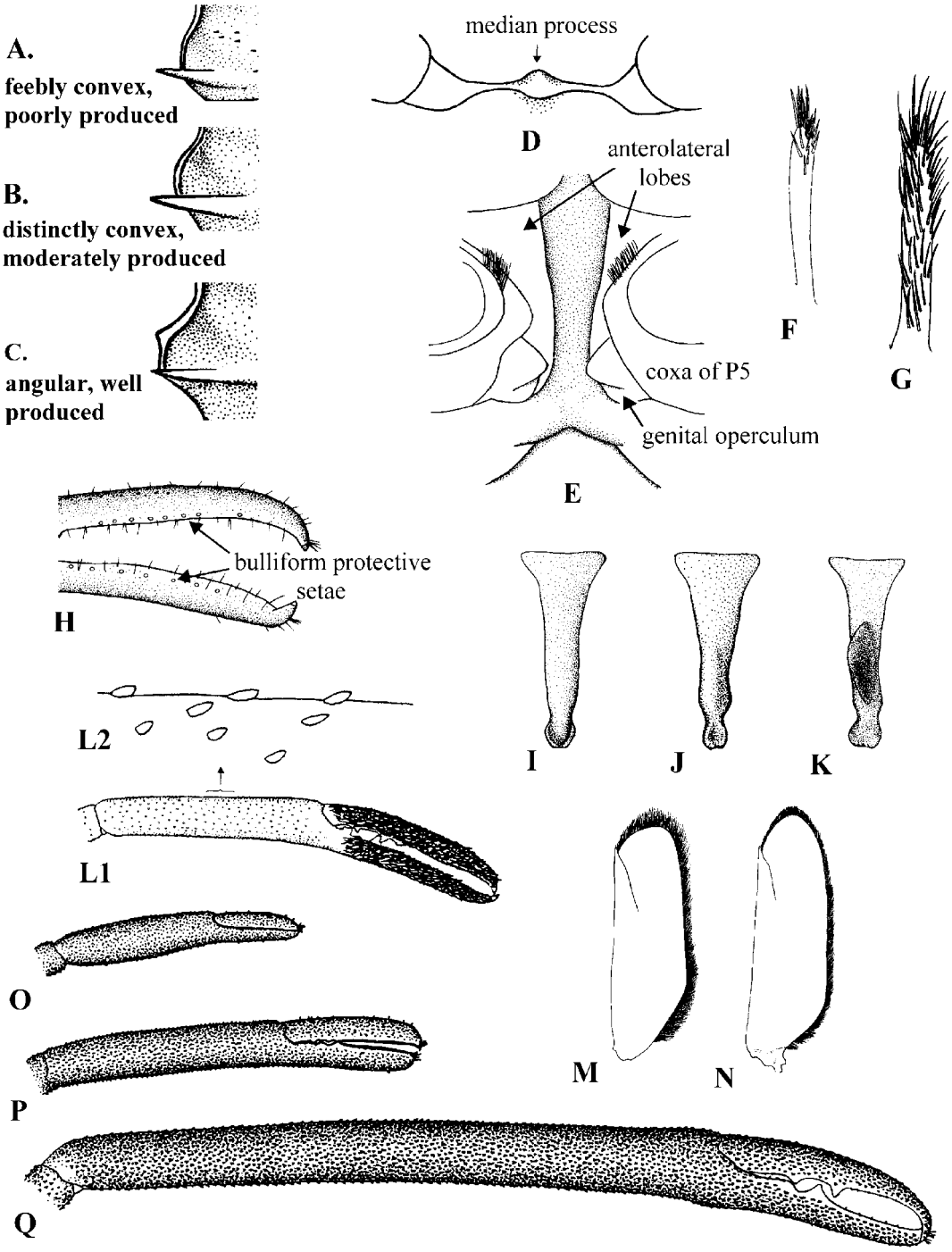

Figure 3. Selected morphological characters. (A–C) variation in shape of inferior orbit, (D) T4 median process, (E) genital operculae on male T8, (F) appendix masculina of immature male, (G) appendix masculina of sexually mature male, (H) bulliform protective setae on lateral cutting edges of fully developed P2, (I) ventral inter-uropodal sclerite without pre-anal carina, (J) ventral inter-uropodal sclerite with low, rounded pre-anal carina (K) ventrolateral view of inter-uropodal sclerite showing high, well-developed pre-anal carina, (L1) protective setation on manus of developed male chela of *M. australiense*, (L2), magnified view of protective setae of same, (M) anterior scaphocerite lamina produced forward at inner angle, (N) anterior scaphocerite lamina strongly produced forward at or near mid-line, (O) undeveloped male chela of *M. tolmerum,* (P) developing male chela of same, (Q), fully developed male chela of same.

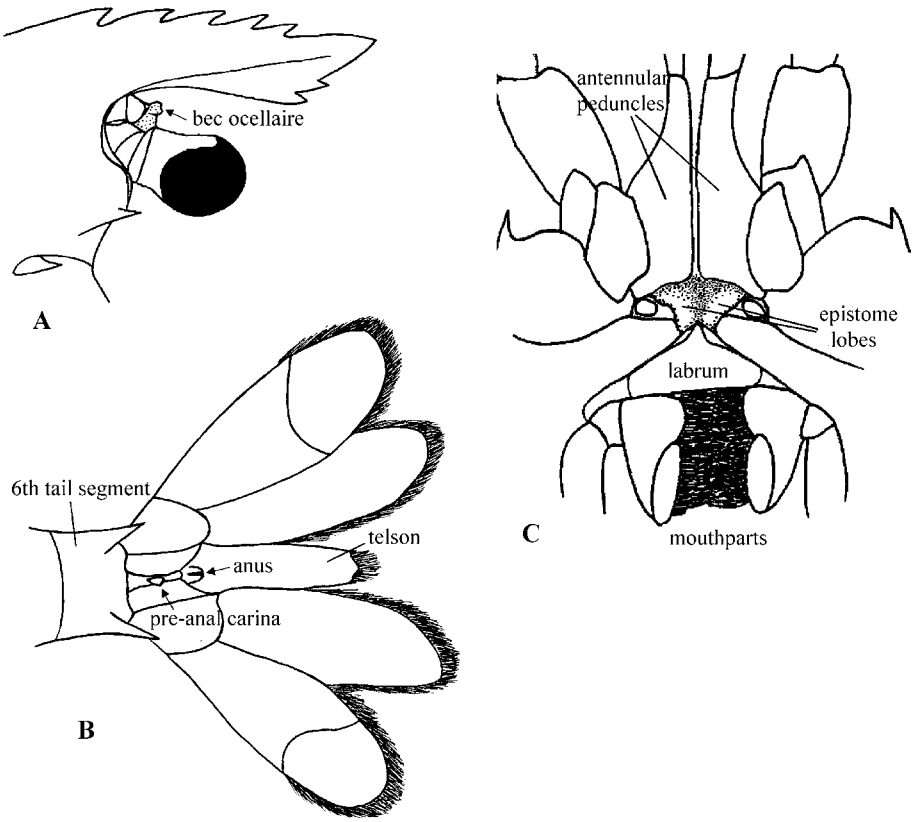

Figure 4. Relative positions of three morphological characters rarely used for the genus prior to this study: (A) bec ocellaire, (B) pre-anal carina on inter-uropodal sclerite, (C) epistome.

behind the segment underneath the telson. The inter-uropodal sclerite in Australian species is either without a pre-anal carina (Fig. 3I), with a low rounded pre-anal carina (Fig. 3J) or with a strongly developed, keel-like pre-anal carina (Fig. 3K).

Spines and setae

In the past there has been considerable inconsistency in the usage of the terms spine, tooth and seta in descriptions of cuticular processes in *Macrobrachium* and other decapod crustaceans. This was previously noted by Felgenhauer (1992), 'Strict limiting definitions for cuticular surface specialisations are difficult to produce and have not really been accurately defined. What one investigator may consider a spine could be a strong seta of another investigator'.

According to Watling (1989), a seta is 'an articulated [with a basal socket] cuticular extension of virtually any shape or size' whereas a spine always lacks a basal socket. By this definition many of the spines, spinules, tubercles and scales described by previous authors on the second chelipeds and body of *Macrobrachium* are clearly setae. An appraisal of cuticular processes in *Macrobrachium* during this study indicated that setae generally have a cuticle of different appearance to the surrounding integument i.e. more heavily tanned or less pigmented. By contrast spines and teeth often have an integument similar to the surrounding cuticle, apart from the tip which may be heavily tanned. Although moveable spines and teeth (Fig. 5B) may superficially appear to be articulated at the base, they instead have a basal suture (an area of flexible cuticle) which allows the spine or tooth to flex in relation to surrounding cuticle. Immoveable spines/teeth (Fig. 5A) lack this suture. In many species of *Macrobrachium* the posterodorsal rostral teeth of juveniles and young adults are moveable (with a complete basal suture) but the suture decreases in length

with age until in fully developed males the teeth are immoveable or submoveable (with an incomplete basal suture).

Several systems for the classification of setae have been proposed. Some of the more recent classifications include those of Thomas (1970), Jacques (1989), Watling (1989) and Felgenhauer (1992). The following classification of seta in *Macrobrachium* is largely based on the setal types diagnosed by Thomas (1970) and Felgenhauer (1992).

Simple setae

Simple setae have smooth setal shafts without setules or scales, an annulus and taper to a sharp point. In *Macrobrachium* several types of smooth setae are evident. The most ubiquitous type of smooth seta is long and moderately stiff with a sharp point (Fig. 5C), a typical bristle. For convenience the term 'simple seta' has been restricted to this type of smooth seta in this study. Simple setae are commonly found on the pereiopods.

Pappose setae

Pappose setae (Fig. 5F) are generally long, fine and thread-like. In *Macrobrachium* they typically occur together in dense clumps on the segments of the second pereiopods, particularly on the chelae where they often form a dense velvety pubescence. The shaft of pappose setae bears numerous long, randomly arranged, setules. In intermoult specimens these setules are frequently covered in fine organic matter. Pappose setae have been commonly referred to as 'woolly' or 'velvety' hairs by previous authors.

Spiniform setae

These are a robust form of smooth seta which are spine-like in appearance (Fig. 5D). In *Macrobrachium*, they usually occur in low numbers in fixed positions on the dorsal and posterior telson, the posterior propodal margins of the ambulatory pereiopods and on the distolateral uropodal exopod. Previous authors have generally referred to spiniform setae as spines or spinules.

Protective setae

The stout smooth setae abundant on the segments of the second pereiopods in developed male *Macrobrachium* appear to be unique in the family, apart from species currently assigned to *Cryphiops*. In developed males of many species these setae are also found on the anterolateral carapace and abdomen. Unlike spiniform setae, which tend to occur in fixed positions in low numbers, these setae are found in large numbers as fields. I have termed them 'protective' setae as they appear to have a defensive function against predators, similar to true spines and teeth. Protective setae show considerable variation in size and shape in *Macrobrachium*. Generally they first appear as small spinule-like buds (Fig. 5K) but increase in relative size as the chelipeds develop. In some species, such as *M. rosenbergii*, the protective setae in fully developed males have raised sockets and are strongly spiniform (Fig. 5H). In others they are flattened and squamiform (Fig. 5J). Other common forms are bulliform (Fig. 5I) and mamilliform (Fig. 5G). Protective setae are always heavily tanned and lack an annulus or basal septum. They have generally been referred to as spines, spinules, tubercles or scales by previous authors.

Plumose setae

This is the most common type of compound seta in decapods. As described by Felgenhauer (1992) plumose setae bear 'two distinct rows of long, usually delicate setules whose insertions are always directly opposite one another on the setal shaft' (Fig. 5E). The shaft is typically devoid of setules towards the base (Thomas, 1970). Plumose setae or 'feathered' setae are commonly found along the margins of natatory appendages such as the pleopods and uropods in *Macrobrachium*. On these appendages plumose setae appear to improve swimming efficiency by extending the effective surface area (Thomas, 1970). An unusual type of plumose seta is sometimes found on the posterior telson of caridean shrimps. Unlike normal plumose setae, the setal shaft is robust and spine-like, with the setules arranged in two rows set at an angle of approximately 90° to each other. The setules are absent near the tip and on the basal third of the setal shaft. These spiniform plumose setae were not seen on *Macrobrachium* or other palaemonine shrimps during this study but are typically found on the posterior telson of many

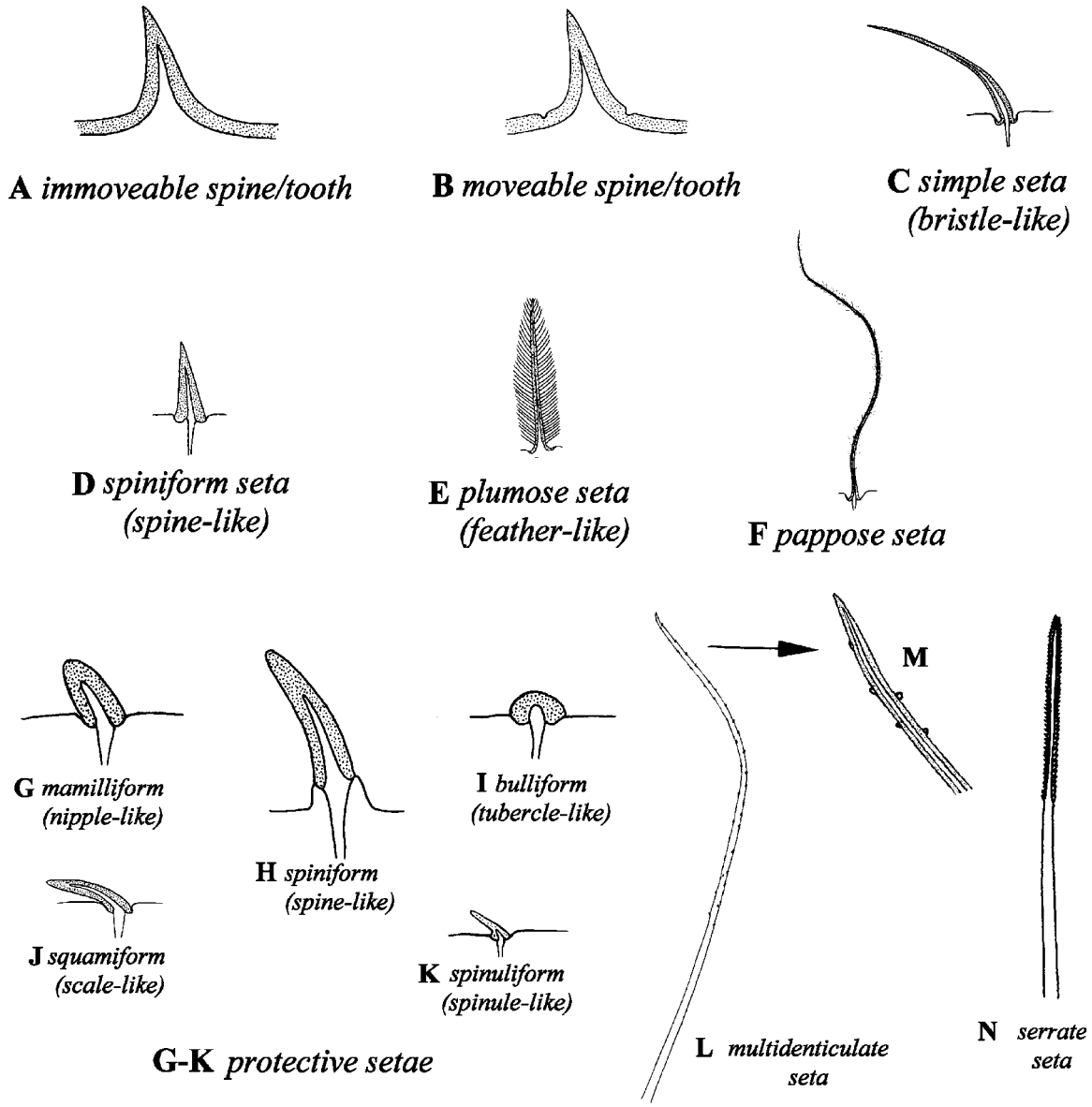

Figure 5. Major spine and setae types in *Macrobrachium* as used in this study. (A–B) Spines (B, moveable spine with basal suture showing as thinner area of cuticle), (C) An unmodified bristle-like, simple seta, (D-O) Various types of modified setae, (D) Spiniform seta, as found on dorsal surface and posterior margin of telson, (E) plumose seta, as commonly seen fringing natatory appendages, (F) pappose seta from pubescence on P2, (G–K) types of protective setae, as found on P2, carapace or abdomen, (L) multidenticulate seta from fingers of minor P2 chela of developed male of *M. latidactylus*. M, enlarged view of tip from figure L, (N) serrate seta from terminal segment of third maxilliped in *M. lar*.

species in the subfamily Pontoniinae. They also occur on the posterior telson of species of *Caridina*. In the literature they are often referred to as spines.

Serrate setae

This is another very common type of compound seta characterised by the presence of sharp, relatively short, denticules arising from the setal

shaft and a basal septum. The denticules always arise distal to a well-developed annulation halfway along the shaft (Thomas, 1970). Serrate setae are commonly found on appendages important in grooming the exoskeleton (Felgenhauer, 1992). Typical serrate setae (Fig. 5N) have serrations arranged in two opposite rows, set at approximately 45° to one another, gradually falling to the horizontal distally (Thomas, 1970). These setae typically occur on the terminal segment of the third maxilliped and proximal propodus/distal carpus in *Macrobrachium*. In palaemonines, the penultimate segment and ischiomerus of the third maxilliped have a type of serrate seta which have much finer, more closely spaced serrations.

Multidenticulate setae

This type of compound seta is common on the minor second pereiopods of a number of species. Typically, they are restricted to the cutting edges of the fingers, but in some cases are also found elsewhere on the minor cheliped. Unlike serrate setae, the denticules or scales are placed around the shaft in a random or spiral pattern (Fig. 5L, M). This type of seta appears to be a synapomorphy for a natural group that includes *M. latidactylus*, *M. bariense*, *M. handschini*, *M. papuanum*, *M. olfersii*, *M. felicinum*, *M. zariquieyi* and *M. faustinum*. Multidenticulate setae also occur on the third maxilliped in *M. scabriculum* (Heller, 1862a, b).

Systematics

Genus ***Macrobrachium*** Bate, 1868

Macrobrachium Bate, 1868, p. 363 (in part) [type species, *Macrobrachium americanum* Bate, 1868, selected by Fowler, 1912. Gender: neuter].

Eupalaemon Ortmann, 1891, p. 696 [type species, selected by Holthuis, 1955, *Palaemon acanthurus* Wiegmann, 1836. Gender: masculine].

Parapalaemon Ortmann, 1891, p. 696 [type species, selected by Holthuis, 1955, *Palaemon dolichodactylus* Hilgendorf, 1879 (=*Palaemon scabriculus* Heller, 1862), Gender: masculine].

Macroterocheir Stebbing, 1908, p. 39 [type species, by monotypy, *Palaemon lepidactylus* Hilgendorf, 1879. Gender: masculine].

Diagnosis

Cephalon. Rostrum laminiform, with dorsal, ventral and lateral carinae; dorsal and ventral carinae dentate, interspaces setose, setae plumose, marginal along dorsal carina, submarginal on ventral carina, dorsal acumen typically with number of long simple setae. Ocular cornea globular, slightly depressed, typically with accessory pigment spot, inferior orbit moderately produced, angular or rounded (indistinctly produced, appearing truncate in *M. latidactylus*). Bec ocellaire moderately to well developed (indistinct in *M. placidulum*). Lower antennular flagellum simple, upper flagellum with two rami, rami fused basally. Distal scaphocerite lamina clearly overreaching distolateral process.

Carapace subcylindrical (almost cylindrical and slightly inflated in large species such as *M. rosenbergii* and *M. lar*), armed with hepatic and antennal spines, hepatic spine moderately to strongly developed, reduced and occasionally absent on one or both sides in some species (*M. hendersoni* (De Man, 1906), *M. hildebrandti* (Hilgendorf, 1893), *M. pilimanus* (De Man, 1892), *M. koombooloomba* sp. nov. (this study)), typically submovable (with incomplete basal suture), freely moveable in some species (with complete basal suture). Antennal spine submarginal, projecting clearly beyond carapace margin, strongly developed (reduced in size in some species e.g. *M. koombooloomba* sp. nov., this study). Branchiostegal groove well developed. Branchiostegal suture distinct, located above and anterior to branchiostegal groove, running directly from hepatic spine to antennal carapace margin. Anterolateral branchiostegite rounded or bluntly angular.

Mouthparts. Mandible with three-segmented palp (two-segmented in *M. cavernicola* and occasionally in other species), molar process well developed, incisor process well developed, tricuspidate, cusps more or less equal in size. Metastoma feebly cleft, paragnaths proximally fused forming robust corpus, distally aliform, ala bilobed, upper lobe with medial groove (sometimes feeble), ante-

rodistally revolute, accommodating mandibular incisor process, corpus with opposing submedial carinae. Maxillula palp bilobed, proximal lobe hooked, bearing setose tubercle/s, functionally coupled with distal paragnath. First maxilliped exopod with flagellum, epipod bilobed, basal and coxal endites distinct. Second maxilliped operculiform, dactylus and propodus strongly expanded, directed posteriorly, covering anterior mouthparts, basis with deep mesial concavity to accommodate abducted distal segments. Third maxilliped pediform, elongated, slender except for distally broadened ischiomerus, well-developed brush of serrate setae on mesial terminal segment, scattered finely serrate setae present on penultimate segment and ischiomerus, ischiomerus and basis fused.

First chelipeds (P1). Shorter and more slender than P2, carpus or palm reaching distal end of scaphocerite, carpus the longest segment, finger tips unguiculate (sometimes feebly).

Second chelipeds (P2). Long or of moderate length, exceeding length of P3–P5, larger and more developed in dominant males (more developed in females in *M. ohione*), without true spines but instead armed with numerous protective setae (= tubercles, scales, spinules or spines of previous authors) in developed male specimens, protective setae resembling spines in some species where the setal alveolus is elevated, finger tips uncinate, unguiculate, cutting edges obviously dentate in fully developed males, not pectinate, manus half length of carpus or greater.

Ambulatory legs (P3–P5). Dactyli unguiculate in adults, of moderate length, ventral margin of propodus bearing series of spiniform setae, without plumose setae, distal propodus of P5 with grooming brush of serrate setae posteroventrally.

Thoracic sternum. Male thoracic sternite 2 unarmed; sternite 4 typically with well developed median process (sometimes feeble or absent); sternite 8 with distinct anterolateral lobes, posteriorly with or without median process in fully developed males; sternites 6–8 with degree of separation between coxae more or less equal. Male genital pore located on papilla arising from inner articular membrane of P5, tip of papilla with well developed operculum.

Abdomen. Tergite 3 slightly convex anteroposteriorly, appearing evenly rounded in lateral view. Telson triangular, narrowing markedly from base to tip, generally stout or of moderate length, length generally less than four times basal breadth in developed males; anterodorsally with semicircular median clump of simple setae; generally with prominent dorsoposterior projection medially, dorsoposterior projection bearing number of simple submedial setae; ventroposterior margin bearing two pairs of spiniform setae, innermost pair the largest, moderately long (clearly less than one third length of telson in adults), typically with more than two plumose setae between innermost pair of spiniform setae; distolateral process of uropodal exopod with accessory spiniform seta mesially (lost in some species, e.g. *M. koombooloomba* sp. nov., this study).

PL1 endopod clearly shorter than exopod, distally ovate. Appendix internae well developed on PL2 to PL5, absent on PL1. Appendix masculina distinctly shorter than endopod, with distinct anterior face, moderately flexible, bearing numerous simple setae on anterior face and tip.

Developmental variation

The rostrum is generally much longer and more slender in juveniles and decreases in relative length with age. In large species, such as *M. rosenbergii*, the difference in length can be extreme. Curvature of the rostrum is also more developed in young specimens. The proximal dorsal rostral teeth are often moveable (complete basal suture) or submoveable (incomplete basal suture) in juveniles but the basal suture progressively shortens until in fully developed males the teeth are fused to the rostrum (without basal suture) in many species. In some species a number of proximal teeth remain moveable or submoveable.

The hepatic spine on the carapace is often moveable in juveniles but in adults the basal suture is incomplete and the spine is submoveable. In a few species it remains freely moveable.

Carapace protective setation develops with age, being most developed in dominant males. In many species the carapace remains glabrous. The cephalothorax and abdomen are more slender and always glabrous in juveniles. In females the body generally remains smooth but in males the anterolateral carapace, telson and lateral surfaces of the abdominal pleura may bear protective setae. These

usually appear in developed males, being most developed in dominant individuals. The median process on T8 is sharper and more distinct in undeveloped males. In fully developed males it is low and rounded or absent. The anterolateral lobes on male T8 become progressively larger and less separated as males develop.

The first pereiopods increase in length relative to body size according to individual dominance status and sexual maturity, being longest in fully developed males.

The second pereiopods vary greatly in degree of development according to sex and individual dominance. In fully developed males these appendages are markedly enlarged whereas in undeveloped, subordinate males they resemble those of females. Once sexually mature, development of the second pereiopods in an individual is somewhat independent of age and depends more on the number of dominant males in a population, the availability of resources, and the individual's relative rank. In overcrowded populations in a diminishing resource, such as a drying waterhole, there are generally few developed males and many subdeveloped or undeveloped males. Developed males in such situations also tend to have a more 'stunted' body size. Upon the loss of a dominant male another subdeveloped male generally takes on the characteristics of a developed dominant male at the next moult. In areas where resources are less limited, such as large, permanently flowing rivers, there are often many developed males of a large body size.

In the wild, males with one or both chelipeds regenerating or absent are common. A fully developed male which has lost its chelipeds during an agonistic encounter develops chelipeds resembling those of an undeveloped male at the next moult. Generally at least two or more moults are required for the chelipeds to fully re-develop. Dominant males which have lost one or both chelipeds also lose their rank in the dominance order and may not re-develop fully if there are already too many dominant males in the area.

According to Henderson and Matthai (1910), the development of the second pereiopods in males generally occurs as follows: 'the ischium grows more slowly than the merus, the merus and carpus grow with the same rapidity, the palm grows faster than the carpus and the fingers grow less rapidly than the palm and slightly faster than the merus and carpus.'

In many species the palm of juveniles is relatively inflated and the fingers are long, slender and somewhat mesially curved. The fingers are always non-gaping, strongly carinate along the cutting edges and without teeth. Protective setae and pappose setae are absent. Protective setae develop in size with age and increased dominance in males. In species where a thick pappose setal pubescence is present on the fingers, the pubescence develops from the cutting edges of the fingers outwards and becomes progressively thicker. Teeth on the cutting edges also develop progressively as the medial carina diminishes in size (generally towards the finger tips). Developed males lack a medial carina and have well-developed teeth on the cutting edges (at least proximally). The manus, carpus and merus of the second pereiopods become more robust and are often inflated in fully developed males. In species which have a gape between the fingers in developed males the fingers of juveniles are non-gaping.

The third to fifth pereiopods increase in relative length according to individual dominance and sexual maturity, being longest in fully developed males.

The appendix masculinae generally appear after the development of the genital operculae in males. At first, the appendix masculina is relatively small, flexible and sparsely setose (Fig. 3F). Setation develops until the anterior face is covered with numerous simple setae in developed males fig. 3G. The appendage also becomes more robust and less flexible.

From the above account it is clear that body size is a poor indication of whether a male is fully developed and dominant. There lies one of the major problems which has confronted all *Macrobrachium* taxonomists. Apart from relative body size how is it possible to gauge whether the chelipeds are fully developed when describing species? To highlight the problem, almost half of the new taxa described in the Indo-West Pacific since the last major revisionary work of Holthuis (1950) appear to be based on undeveloped or developing males. In an attempt to overcome this problem I have constructed the following key to male developmental stages.

Key to male developmental stages

(Note: males identified by genital operculum on articular membrane of P5, Fig. 3E)

1. Appendix masculina on endopod of second pleopod well developed, anterior face and tip densely setose (Fig. 3G)..... 2
– Appendix masculina on endopod of second pleopod absent or poorly developed anterior face and tip sparsely setose or setose at tip only (Fig. 3F).
.....*undeveloped males* (sexually immature)

2(1). P2 enlarged, longer or more robust than females, protective setae (= tubercles, spinules, spines, scales of previous authors) conspicuous (Figs 3L1, L2), teeth on proximal cutting edges of fingers distinct 3
– P2 not enlarged, of about same length and shape as females, protective setae absent or inconspicuous, teeth on proximal cutting edges of fingers absent or indistinct.
.....*undeveloped males* (sexually mature)

3(2). P2 with teeth on proximal cutting edges of fingers distinct but not fully developed and/or pappose setal pubescence on fingers sparse (when applicable) and/or submedian rows of bulliform (tubercle-like) protective setae on cutting edges indistinct (when applicable) and/or protective setae on body poorly developed (when applicable).
. ..... *developing males* (sexually mature)
– P2 with teeth on proximal cutting edges of fingers strongly developed, well developed pappose setal pubescence on fingers (when applicable), well developed submedian rows of bulliform protective setae on cutting edges of fingers (when applicable), strongly gaping fingers (when applicable) and well developed protective setation on body (when applicable).
.....*fully developed males* (sexually mature)

Remarks

In his key to genera and subgenera of Palaemoninae, Holthuis (1950) distinguishes *Macrobrachium* from related palaemonine genera using the following features: (1) carapace with hepatic spine, without branchiostegal spine; (2) mandible with palp; (3) dactyli of last three legs simple. Chace & Bruce (1993) added the following characters in their key to Indo-West Pacific genera of Palaemoninae to help separate *Macrobrachium* from *Brachycarpus*: (1) carapace with branchiostegal suture; (2) first pleopod of male without appendix interna on endopod.

The presence of a hepatic spine was used by Holthuis (1952b) as the criterion for re-assigning *Leander intermedius* Stimpson, 1860 to *Macrobrachium*. Recently, Walker & Poore (2003) transferred *Leander intermedius* Stimpson from *Macrobrachium* to *Palaemon* and broadened the diagnosis of *Palaemon* to accommodate species with a spine on the carapace in hepatic or intermediate position between typical branchiostegal and hepatic positions. Similarly, the presence or absence of the hepatic spine is not a strong character to distinguish *Macrobrachium* from *Cryphiops*. There is a trend towards reduction and loss of the spine in some freshwater species of *Macrobrachium*, e.g. *M. hendersoni* (De Man, 1906), *M. hildebrandti* (Hilgendorf, 1893), *M. pilimanus* (De Man, 1892), and *M. koombooloomba* sp. nov. (this study).

The presence or absence of a mandibular palp also appears to be a poor generic character. In some *Palaemon*/*Palaemonetes* species the mandibular palp may be present, reduced in length or absent within the same population (Fujino & Miyake, 1968; Chace, 1972; Boulton & Knott, 1984; Bray, 1976).

During the course of this study, 100 of approximately 210 currently recognised species of *Macrobrachium* were examined, including the type species, *M. americanum*. The type species of the related palaemonine genera, *Brachycarpus*, *Cryphiops*, *Palaemon*, *Palaemonetes*, and *Pseudopalaemon* have also been examined. On the basis of these comparative studies I believe that *Macrobrachium sensu stricto* can be best distinguished from related genera by the following characters:

1. Well-developed sexual dimorphism of the second pereiopods which are also greatly enlarged in fully developed males (except in *M.*

ohione where adult females have larger chelipeds).

2. Second pereiopods of developed males covered with distinct protective setation (protective setation poorly developed or absent in females and undeveloped males).
3. Cutting edges of fingers on developed male second pereiopods with well developed teeth (at least proximally) in fully developed males.
4. P2 manus of moderate length or long, at least half length of carpus.
5. Appendix masculina robust, exceeding the appendix interna in length but clearly shorter than the endopod, anterior face with numerous long simple setae in developed males.
6. Tricuspidate mandibular incisor processes.
7. Male thoracic sternites T6 to T8 equally separated medially. T8 with well developed anterolateral lobes, with or without medial process posteriorly (generally more developed in young males).
8. More than two pairs of plumose setae between the innermost pair of spiniform setae on the posterior telson margin. Plumose setae not continuing laterally past outermost pair of spiniform setae.
9. Branchiostegal suture distinct, located above and anterior to branchiostegal groove, running directly from hepatic spine in typical hepatic position to antennal carapace margin.
10. No appendix interna on the endopod of the first male pleopod.
11. Last three pereiopods with simple dactyli, without plumose setae.
12. Abdominal tergite 3 slightly convex antero-posteriorly (abdomen evenly rounded in lateral view).
13. Distal propodus of P5 with brush of grooming setae posteroventrally.
14. P4 and P5 not extremely long and slender, shorter than P2 in adults.

Table 1. List of nominal species currently assigned to *Macrobrachium* but atypical in one or more features. Those with an asterisk possibly based on undeveloped males

Indo-West Pacific
Bithynis? hildebrandti Hilgendorf, 1893*
Macrobrachium edentatum Liang and Yan, 1986*
M. glabrum Holthuis, 1995*
M. guangxiense Liang and Yan, 1981*
M. inflatum Liang and Yan, 1985*
M. jiangxiense Liang and Yan, 1985*
M. mieni Dang, 1975*
M. palaemonoides Holthuis, 1950
M. pinguis Dai, 1984*
M. sankollii Jalihal & Shenoy in Jalihal et al., 1988
M. srilankense Costa, 1979*
Palaemon banjarae Tiwari, 1958
P. canarae Tiwari, 1958
P. kistnensis Tiwari, 1952
P. mirabilis Kemp, 1917
P. naso Kemp, 1918
P. peguensis Tiwari, 1952
P. riukiuensis Kubo, 1940*
P. superbus Heller, 1862*
Palemon (sic) *lamarrei* H. Milne Edwards, 1837
East Pacific
M. acherontium Holthuis, 1977*
West Atlantic
M. catonium Hobbs & Hobbs, 1995*
M. depressimanum Pereira, 1993
M. dierythrum Pereira, 1986*
M. pectinatum Pereira, 1986
M. pumilum Pereira, 1986
M. reyesi Pereira, 1986
M. rodriguezi Pereira, 1986
M. villalobosi Hobbs, 1973
P. jelskii Miers, 1877
P. (*Eupalaemon*) *praecox* J. Roux, 1928
Mediterranean
P. niloticus P. Roux, 1833

Of the species currently assigned to the genus, at least 31 do not fit this definition (Table 1). Fourteen species may prove to be based on undeveloped males and show differences only in the first three characters. The possibility exists that some *Macrobrachium sensu stricto* lack sexual dimorphism of the second pereiopods and retain smooth chelipeds as developed males, particularly in blind cave species where agonistic behaviour may be reduced. However, this conclusion may only be reached after an examination of a good series of specimens of different sizes for each of these species.

The remaining species in Table 1 differ significantly in a number of the above characters and appear wrongly assigned to the genus. The polyphyly of *Macrobrachium senus lato* has been

demonstrated by Pereira (1997). In his cladistic analysis of freshwater shrimps of the family Palaemonidae, several of the West Atlantic species mentioned in Table 1 formed a distinct clade with species of *Pseudopalaemon* (viz. *M. depressimanum* Pereira, 1993, and *M. pectinatum*, *M. pumilum*, *M. reyesi*, and *M. rodriguezi* all of Pereira, 1986). The generic status of these species require re-evaluation.

I have also compared *Cryphiops caementarius* (Molina) with *M. americanum* Bate, the type species of *Macrobrachium*. In my opinion the only significant difference between *C. caementarius* and *Macrobrachium* is the arrangement of plumose and spiniform setae on the posterior telson (see character 8 above). The presence or absence of a hepatic spine, as used by Holthuis (1952a), is of doubtful value as a distinguishing generic character. As previously mentioned, there appears to be a trend towards reduction and loss of this spine (may be absent on one or both sides in some individuals) in a number of freshwater species of *Macrobrachium* (e.g. *M. hendersoni* (De Man, 1906), *M. hildebrandti* (Hilgendorf, 1893), *M. pilimanus* (De Man, 1892), *M. koombooloomba* sp. nov. (this study)). Apart from *C. caementarius*, other species currently assigned to the genus in the subgenus *Bithynops* appear remarkably similar to *Macrobrachium*.

Although *C. caementarius* in many ways appears congeneric with *Macrobrachium*, synonymising the two taxa would cause a number of problems. *Cryphiops* Dana has priority over *Macrobrachium* Bate, but the latter name is well established and almost universally used in recent times. One exception is Johnson (1966) who used *Cryphiops* as a senior synonym of *Macrobrachium*. If the current classification is retained, *C. caementarius*, is at least a highly distinctive species. By contrast, the species currently assigned to *Cryphiops* (*Bithynops*) by Villalobos et al. (1989) do not appear to show any significant differences from *Macrobrachium*, apart from the absence of a hepatic spine.

Ortmann (1891) divided the genus (as *Palaemon*) into four subgenera: *Eupalaemon*, *Parapalaemon*, *Macrobrachium* and *Brachycarpus* (now given separate generic rank) based on the proportions and shape of segments of the second pereiopods. Despite usage of this classification for a period in the early part of the 20th century by some authors it is now regarded as impractical and untenable (Henderson and Matthai, 1910; Holthuis, 1950).

Taxa excluded from the Australian fauna

Macrobrachium australe (Guérin-Méneville, 1838) – the only record of this species from Australia is based on a junior subjective synonym, *Palaemon danae* Heller, 1865, which was described from Sydney. I have examined topotypical specimens of *Palaemon danae* (identified by Heller) from the collection of the Naturhistorisches Museum Wien and agree with Holthuis (1950) that Heller's nominal species is a synonym of *M. australe*. However, it is very likely that Heller's type locality is incorrect. Sydney lies at the southern coastal limit of the genus in Australia and only *M. tolmerum* Riek, 1951 and *M. novaehollandiae* (De Man, 1908) were recorded from the Sydney area during this study. Despite the large collection of Australian material at my disposal, there were no definite records of *M. australe*. The species recorded by Riek (1951) as *M. danae* does not appear to be *M. australe* based on his description of the second pereiopods and notes on its biology. Riek considered *M. danae* 'restricted almost entirely to salt water though it may enter small freshwater springs and swamps at the shoreline'. He also noted that 'ovigerous females are normally collected in salt water'. I have been unable to locate specimens of *M. danae* identified by Riek in any Australian museum collection. It is possible that Riek's *M. danae* consists of two species *M. equidens* (Dana, 1852) and *M. tolmerum* (Riek, 1951). Ovigerous females of *M. equidens* are often collected in inshore marine areas and *M. tolmerum* is commonly found in coastal freshwater springs and swamps.

Traditionally, *Macrobrachium* keys have relied heavily on the morphology of the rostrum and developed male chelipeds (De Man, 1892; Holthuis, 1950, 1952a; Chace & Bruce, 1993). Generally this meant only developed males could be successfully identified. Unfortunately only a small percentage of the total number of individuals collected from any given locality may be developed males. The chelipeds are also easily broken off during handling and preservation.

Unlike previous keys, the following key has been designed to be used with all adult specimens, not just developed males. The morphology of the chelipeds are still used in several couplets but always in combination with other characters. Where several characters are given in a couplet each is of equal weighting.

The key will work satisfactorily with juveniles of some species, particularly larger juveniles. However, in most cases adult specimens are necessary for reliable identifications. The key should also be used in conjunction with the 'key to male developmental stages' provided earlier.

Due to the high variability inherent among species of the genus, a small percentage of specimens will not key correctly. It is important therefore that all keyed specimens should be checked closely against the figures, diagnoses, maximum size and distribution maps provided in the species accounts to verify the identification. Couplets 3 and 4 of the key are trichotomous whereas the remaining couplets are dichotomous.

Key to Australian *Macrobrachium*

Note: third and fourth couplets of key are trichotomous

1(0). Scaphocerite anterior margin produced forward at inner angle (Fig. 3M) or less commonly, evenly rounded, not strongly produced forward at or near mid-line; velvety pappose setal pubescence, if present on fingers of developed male P2, not restricted to dactylus 2

– Scaphocerite anterior margin strongly produced forward at or near mid-line (Fig. 3N); developed male P2 with velvety pappose setal pubescence on dactylus, absent on fixed finger (Fig. 16H). ..... *M. rosenbergii* (Figs 16–18, 36L, M) [Large, euryhaline species (non-ovigerous adults in fresh waters) up to 320 mm TL. Wide-ranging Central Indo-West Pacific: Fitzroy R., W.A. to Normanby R., NE.Qld (Fig. 18).]

2(1). First ventral rostral tooth located in proximal half or at about mid-length of ventral carina; thoracic sternite 4 (between first pereiopods) with distinct median process (rounded or spinate; Fig. 3D) 3

– Ventral rostral carina unarmed on proximal half, first tooth located clearly within distal half (Fig. 23B); thoracic sternite 4 without median process. ..... *M. koombooloomba* sp. nov. (Figs 23, 24, 36A) [Small, freshwater species up to 65 mm TL. Upper Tully R. basin, NE Qld (Fig. 24).]

3(2). Inter-uropodal sclerite (between ventral uropods) without pre-anal carina Fig. 3I; fingers of developed male P2 without pappose setal pubescence or, if present, distal cutting edges non-crenulate; developed males with protective setation (spinule or tubercle-like) on anterolateral carapace (e.g. Fig. 6B); developed ova (eye spots visible) small to moderately large (0.6–1.6 mm maximum length) 4

– Inter-uropodal sclerite with strongly keeled, well-developed pre-anal carina (Fig. 3K); fingers of developed male P2 without pappose setal pubescence, distal cutting edges non-crenulate; developed males without protective setation on anterolateral carapace; developed ova small, 0.6 mm maximum length 9

– Inter-uropodal sclerite with poorly to moderately developed pre-anal carina, rounded rather than strongly keeled (Fig. 3J); developed male P2 with pappose setal pubescence covering fingers (pubescence develops from cutting edges in developing males to completely covering fingers in fully developed males), distal cutting edges crenulate in developed males; developed males without protective setation on anterolateral carapace; developed ova moderately large, 1.4 mm maximum length..... *M. australiense* (Figs 19–22, 36D) [Medium-sized, freshwater species up to 91 mm TL. Widespread throughout most of northern, central and eastern Australia (Fig. 22).]

4(3). Inferior orbit moderately or well produced, angular, post-antennular carapace margin generally concave (rarely straight) fig. 3C; developed males with protective setation on

carapace and abdomen; developed ova small to moderately large, 0.6–1.4 mm maximum length 5

– Inferior orbit moderately produced, obtuse, post-antennular carapace margin distinctly convex and evenly rounded (Fig. 3B); developed males with protective setation on carapace, absent on abdomen; developed ova moderately large and few, 1.6 mm maximum length. ..... *M. handschini* (Figs 33–35, 36H, I) [Small, freshwater species less than 65 mm TL. Northern Australia; Victoria R. basin, N.T. to Normanby R. basin, Qld: southern New Guinea (Fig. 35).]

– Inferior orbit poorly produced, appearing truncated, post-antennular carapace margin slightly convex or straight (sometimes slightly concave) (Fig. 3A); developed males with protective setation on carapace, absent on abdomen; develop ova small and numerous, 0.6 mm maximum length. ..... *M. latidactylus* (Figs 31, 32) [Small, euryhaline species (adults in estuarine and lowland fresh waters) up to 80 mm TL. Wide-ranging Central Indo-West Pacific (Fig. 32).]

5(4). P2 chela clearly longer than carpus in adults (may be equal to carpus in juveniles); pappose setal pubescence, if present on fingers, not extensive on lateral dactylus and restricted to cutting edge of propodus in developed males..... 6

– P2 chela clearly shorter than carpus in developed males (Fig. 10E), equal in length to slightly longer than carpus in females and undeveloped males, pappose setal pubescence extensive on lateral dactylus but restricted to cutting edge of propodus in developed males (Fig. 10I). ..... *M. idae* (Figs. 10, 11, 36F) [Medium-sized, euryhaline species (adults in estuarine and lowland fresh waters) up to 110 mm TL. Wide-ranging Indo-West Pacific (Fig. 11).]

6(5). P2 without pappose setal pubescence on fingers of subdeveloped/developed males, developed males with submedial rows of bulliform (tubercle like) protective setae on cutting edges of fingers (Fig. 3H); adults generally found in fresh waters 7

– P2 with obvious pappose setal pubescence on fingers (cutting edges at least) of subdeveloped/developed males, developed males without submedial rows of bulliform protective setae on cutting edges of fingers; restricted to estuarine and inshore marine waters 8

7(6). Adult P3 long, propodus easily reaching distal end of scaphocerite; second chelipeds isomorphic; developed ova small and numerous, maximum length 0.6 mm. ..... *M. mammillodactylus* (Figs 12, 13) [Moderately large, euryhaline species (adults in lowland fresh waters) up to 137 mm TL. Wide-ranging Central Indo-West Pacific (Fig. 13).]

– Adult P3 short, reaching distal end of scaphocerite by base of dactylus at most; second chelipeds clearly unequal in length, minor cheliped failing to reach distal end of manus of major cheliped; developed ova moderately large and few, maximum length 1.4 mm. .....*M. bullatum* (Figs 14, 15, 36B) [Small, freshwater species less than 75 mm TL. Northwest Australia: Lennard R. basin, W.A. to Rosie R. basin, N.T. (Fig. 15).]

8(6). Rostrum generally straight and deep, dorsal teeth subequally spaced (Fig. 6B); developed male P2 with pappose setal pubescence on cutting edges of fingers only (Fig. 6I); P2 segments with faint transverse bands in live specimens..... *M. novaehollandiae* (Figs 6, 7, 36J) [Medium-sized, euryhaline, estuarine/inshore marine species up to 120 mm TL. Northern and eastern Australia: Cape Leveque Coasts and Fitzroy R. basins, W.A.; Buckingham R. basin, N.T.; Endeavour R. basin, Qld to Sydney Coast-Georges R. basin, N.S.W. (Fig. 7).

– Rostrum sinuous or upturned, of normal depth, dorsal teeth tending to be more closely spaced proximally above eye than in

distal half (apart from subapical teeth) (Fig. 8B); developed male P2 with pappose setal pubescence completely covering both fingers (Fig. 8E); P2 segments marbled with dark irregular blotches in live specimens. ..... *M. equidens* (Figs 8, 9, 36G) [Medium-sized, euryhaline, estuarine/inshore marine species up to 115 mm TL. Wide-ranging Indo-West Pacific (Fig. 9).]

9(3). Adult P2 merus about equal to or clearly shorter than carpus, fingers clearly less than half length of manus in developed males; epistome lobes not strongly produced anteroventrally in adults (Figs 25C, 27C). 10

– Adult P2 merus clearly longer than carpus (Figs 29F–H), fingers long, clearly greater than half length of manus in developed males (Fig. 29F); epistome lobes strongly produced anteroventrally in adults (Fig 29B). ..... *M. lar* (Figs 29, 30, 36K) [Large, euryhaline species (adults reaching upper catchment fresh waters) up to 195 mm TL. Wide-ranging Indo-West Pacific (Fig. 30).]

10(9). Rostrum short, always failing to reach distal end of scaphocerite, with 11 or more dorsal teeth; developed male P2 in live specimens without distinctive orange ischium. ..... *M. auratum* sp. nov. (Figs 27, 28, 36C) [Small, euryhaline species (adults upstream to mid-catchment fresh waters) up to 80 mm TL. Eastern Qld; Endeavour R. basin to Plane Ck basin (Fig 28).]

– Rostrum of medium length or short (less common), generally over-reaching distal end of scaphocerite, if failing to reach distal end of scaphocerite with 10 or fewer dorsal teeth; developed male P2 in live specimens with distinctive orange ischium. .....*M. tolmerum* (Figs 25, 26, 36E) [Medium-sized, euryhaline species (adults reaching upper catchment fresh waters) up to 120 mm TL. Eastern Australia; Jacky Jacky Ck basin to Hawkesbury R. basin, N.S.W. Also occurs in the Buckingham R. basin, N.T. (Fig. 26).]

Species accounts

Macrobrachium novaehollandiae (De Man, 1908) (Figs 6, 7, 36J)

Palaemon ornatus – Haswell, 1882, p. 196 (not Olivier, 1811)
Palaemon (*Eupalaemon*) *novae-hollandiae* De Man, 1908, pp. 363–370, pl. 16.
Palaemon novae-hollandiae – McNeill, 1926, p. 325.
Palaemon (*Paralaemon*) *aemulus* – Boone, 1935, p. 157, pl. 40 (not Nobili, 1906).
Macrobrachium novae-hollandiae – Holthuis, 1950, pp. 17, 107 (key), 155–156. Riek, 1951, pp. 358, 360.
Macrobrachium novaehollandiae – Healy & Yaldwyn, 1970, pp. 42, 44, fig. 49. Greenwood et al., 1976, pp. 252–286, figs 1–9. Fincham, 1987; p. 353 (key).
not *Macrobrachium novaehollandiae* – Jayachandran & Joseph, 1989, p. 75.

Material examined

Northern Drainage Region. Cape Leveque Coast Basin: AM P2353, Broome; *Fitzroy R Basin*: WAM C21738, Lawley R. mouth; *Buckingham R Basin*: NTM CR007408, Elcho I., Ck near settlement.

Eastern Drainage Region. Endeavour R Basin: QM W18136, Endeavour R., Endeavour Bridge near Cooktown; *Barron R Basin*: QM W19234, Barron R., Kamerunga Bridge; *Johnstone R Basin*: QM W18273, Bamboo Ck mouth, Innisfail; QM W21563, Johnstone R., Innisfail; QM W21998, Johnstone R. at hospital bridge, Innisfail; QM W22011, Unnamed creek at Jubilee Grove estate, Innisfail; QM W22007, Unnamed creek near Innisfail; *Murray R Basin*: QM W22055, Fishers Ck near Fishers Landing south of Cardwell; *Black R Basin*: AM P28174, Bluewater Ck near Townsville; *Proserpine R Basin*: QM W22090, Flame Tree Ck between Airlie Beach and Shute Harbour; *Boyne R Basin*: NTM Cr002650, Gladstone; QM W18252, Boyne R., Bruce Hwy crossing near Benaraby; *Burrum R Basin*: QM W20027, Elliott R; *Mary R Basin*: QM W17980, Saltwater Ck, old Marybor-

ough-Hervey Bay Rd bridge; QM W12660, Tinana Ck barrage; *Noosa R Basin*: QM W17981, Big Tuan Ck near Maryborough-Tin Can Bay Rd crossing; QM W16491, Lake Weyba near Noosa; QM W2079, Noosa Hds; *Maroochy R Basin*: QM W14991, Elimbah Ck, 10 km north of Caboolture; QM W16488, Bribie I., 3 km north of Woorim beach; *Pine R Basin*: QM W19311, Pine R. mouth, small creek c. 400 m west of Houghton Hwy; QM W19309, Cabbage Tree Ck, Sandgate Rd; QM W19308, Nundah Ck, Gateway Arterial Rd crossing; QM W14990, Kedron Brook, Toombul overpass; *Stradbroke–Moreton Islands Basin*: QM W21749, Myora Springs, North Stradbroke I.; *Brisbane R Basin*: QM W15546, Boggy Ck, at walking bridge to BP refinery, Myrtletown; QM W19661, Brisbane; QM W95, Brisbane R.; QM W4812, Brisbane R., between Long Pocket and Cockatoo I.; QM W2660, Brisbane R., Indooroopilly; QM W1039, Brisbane R., Chelmer; QM W17229, Brisbane R., South Brisbane; QM W16646, Brisbane R., Norman Ck mouth; W15519, Norman Ck, Wynnum Rd bridge, Norman Park; QM W16404, Norman Ck, Gilan St, Norman Park; *Richmond R Basin*: AM P14445, Ballina; *Clarence R Basin*: AM P17602, Clarence R., Maclean; *Hunter R Basin*: AM P16173, Hunter R.; AM P17928, Hunter R; *Macquarie-Tuggerah Lakes Basin*: AM P14441, Toukley, Tuggerah Lakes; *Sydney Coast-Georges R Basin*: AM P4075, Lane Cove R. near Killara; AM P17840, Broken Bay mouth; AM P25180, Georges R. Parklands, River Rd; *Inshore Marine*: QM W17135, Nudgee Beach near Nundah Ck; QM W7230, Aldershots, Moreton Bay.

Diagnosis

Rostrum. Medium length in fully developed males, developmental range 0.7–1.0 CL, deep at mid-length (maximum depth much greater than dorso-ventral diameter of cornea); dorsal carina generally straight, sometimes slightly convex, more rarely upturned, dentate along entire length, teeth subequally spaced, 9–12 teeth, 2 completely postorbital, all teeth immoveable in fully developed males (number of proximal teeth submoveable in young males and females); ventral rostrum dentate, 3–5 teeth, first tooth generally located in proximal half.

General cephalon. Ocular cornea large, well-pigmented, accessory pigment spot present. Inferior orbit moderately produced, angular, postantennular carapace margin slightly concave. Bec ocellaire strongly developed. Scaphocerite elongated, length greater than three times maximum breadth, lamina distinctly tapering from broadest point to anterior margin, anterior margin produced forward at inner angle. Epistome completely divided into two lobes, lobes rounded.

Mouthparts. Third maxilliped terminal segment clearly shorter than penultimate segment; exopod about equal in length to ischiomerus. Mandibular molar process crowns as figured (Fig. 6D).

Second chelipeds (fully developed male). Larger and more developed than female P2; isomorphic; long, merus reaching distal end of scaphocerite; bearing simple, protective and pappose setae; all segments with abundant well-spaced mamilliform protective setae; pappose setae forming thick short pubescence on submedial cutting edges of fingers; few tufts of simple setae near fingertips; fingers more or less touching along their length; pollex elongated, slender, uncinate at tip, basal pollex not noticeably broadened, slightly narrower than basal dactylus, proximal cutting edge with dentate ridge followed by distinct gap then large tooth, distally entire; dactylus elongated, slender, basally broadened, uncinate at tip, proximal cutting edge with two large teeth, the first opposing ridge of teeth on pollex, the second slightly advanced of large tooth on pollex, distally entire; manus elongated, cylindrical, straight, slightly expanded basally, distinctly expanded distally, maximum breadth c. equal to maximum merus breadth, much longer than dactylus; carpus slightly shorter than chela, elongated, tapered; merus much shorter than carpus, tapered; ischium with well developed median groove on both superior and inferior faces, compressed, narrowed at mid-length.

Third pereiopods (fully developed male). Long, propodus reaching distal end of scaphocerite; mamilliform protective setae abundant on all segments except distal propodus and dactylus; dactylus elongated, length more than four times basal breadth, ventral carina well developed; unguis poorly developed, length less than one-fifth remainder of dactylus.

Thoracic sternum. T4 with well-developed median process, postcoxal flanges situated posterior to and distinct from median process. Fully developed male T8 with anterolateral lobes widely separated

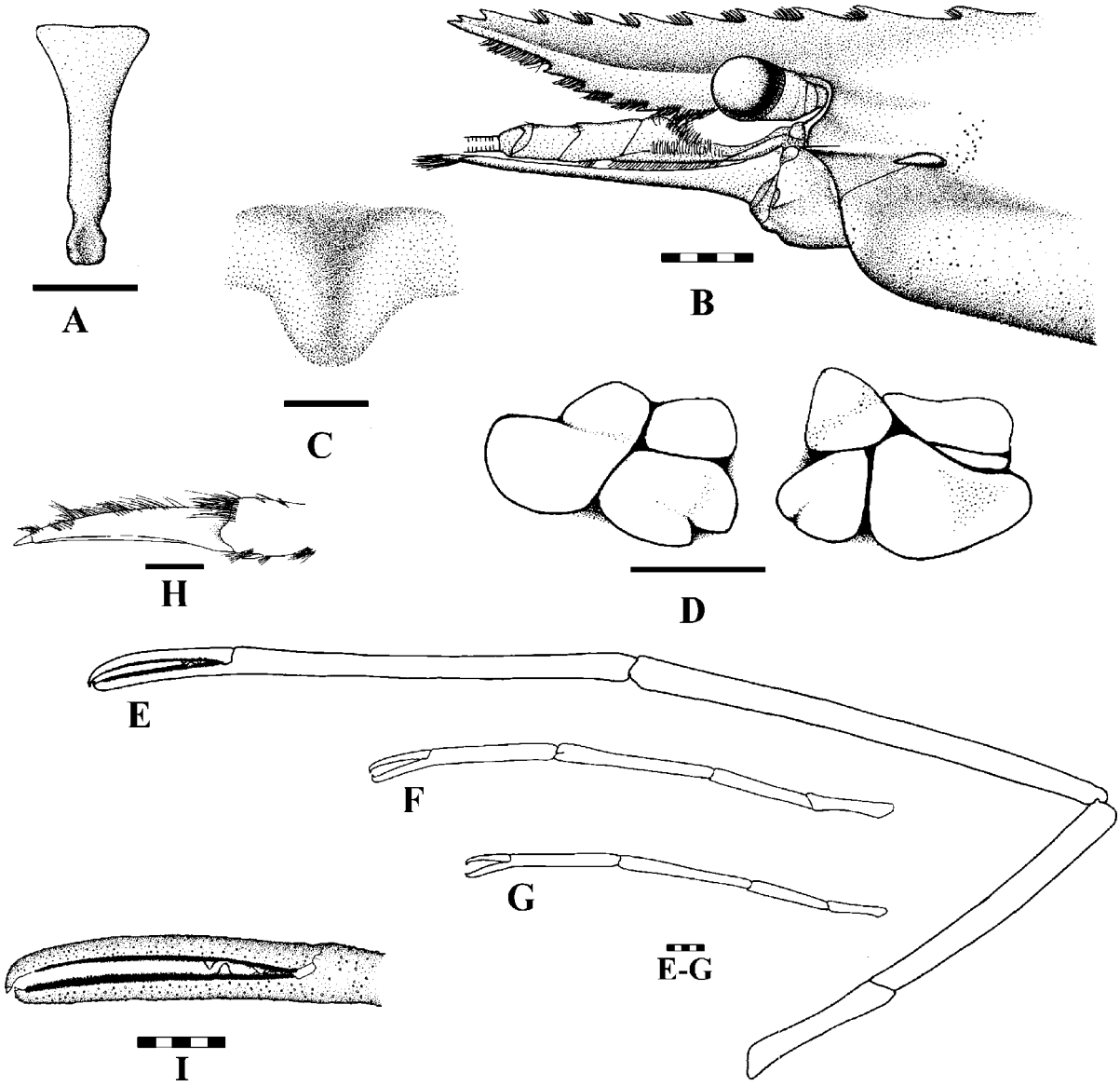

Figure 6. Macrobrachium novaehollandiae (De Man, 1908). (A) QM W95, male 27.0 mm CL, ventral view of inter-uropodal sclerite, (B) QM W2660, male 29.6 mm CL, anterior cephalothorax, (C) QM W16404, male 24.3 mm CL, epistome, (D) crowns of left and right mandibular molar processes (setae omitted) of same, (E) QM W2660, male 29.6 mm CL, fully developed right second cheliped (protective setation omitted), (F) QM W15668, ovig. female 22.3 mm CL, right second cheliped (protective setation omitted), (G) QM W18252, male 12.5 mm CL, undeveloped right second cheliped (protective setation omitted), (H) QM W15668, male 24.9 mm CL, dactylus and distal propodus of right third pereiopod, (I) QM W2660, male 29.6 mm CL, mesial view of fingers and distal manus of fully developed right chela. Solid scale bars and divisions on divided scale bars 1 mm.

posteromedially, median process present posteriorly, process rounded or carinate, spinate in young males.

Abdomen. Inter-uropodal sclerite without preanal carina. Distolateral process on uropodal exopod with accessory spiniform seta mesially.

Body setation (fully developed male). Mamilliform protective setation present on carapace and abdomen, on carapace most conspicuous anterolaterally, on abdomen restricted to lower pleura, tergite 6, uropods and telson.

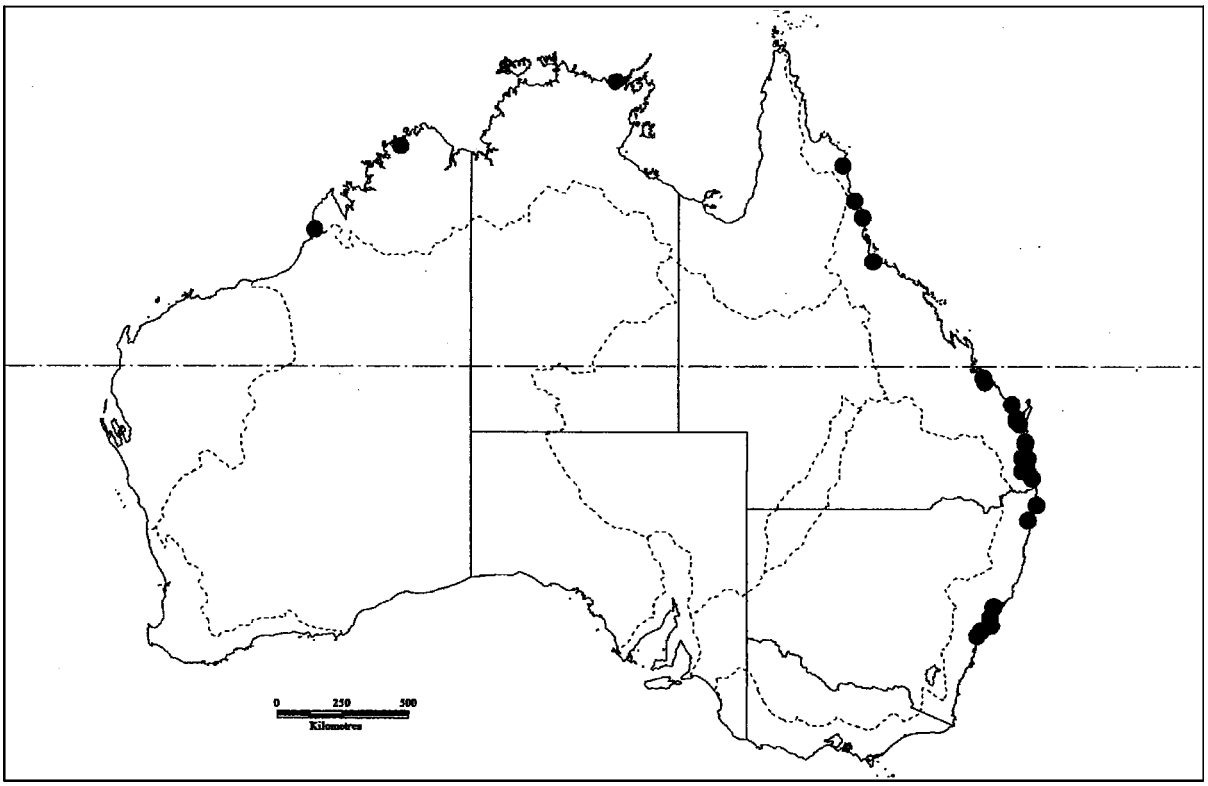

Figure 7. Australian distribution of *Macrobrachium novaehollandiae* (De Man, 1908).

Colour

Antennal flagella translucent, tinged with light olive grey to light pinkish brown, peduncles with pinkish to orange brown specks. Rostrum translucent olive grey to almost clear with pinkish brown to orange brown specks. Ocular peduncles translucent with olive grey to orange brown specks.

Body colour translucent olive grey to light pinkish brown speckled with light orange brown; lateral carapace with distinctive deep olive brown chromatophore stripes; abdominal pleura marked with olive brown on condyles, mottled with dark olive brown in ovigerous females; lateral uropodal exopods orange brown with distolateral process blue grey to olive brown, fringing plumose setae light orange brown.

First chelipeds and ambulatory legs translucent olive grey mottled with deep olive brown, joints of segments orange brown, dactyli translucent olive grey. Second chelipeds olive yellow to olive green, marked with faint olive brown transverse bands or blotches.

Undeveloped ova olive to olive grey.

Life cycle

Euryhaline, 0–33 ppt salinity, adults estuarine but also known from inshore marine areas; eggs small and numerous, up to 3742 per brood (Greenwood et al., 1976), maximum length of developed ova 0.9 mm; ovigerous females collected in estuarine areas; larval development extended, 10 planktonic stages, 41–58 days to metamorphosis at 23 ppt salinity/15–28 °C (Greenwood et al., 1976).

Size

Medium-sized species. Maximum size of developed male 32 mm CL, 120 mm TL. Maximum size of

female 24 mm CL, minimum size of ovigerous female, 9 mm CL.

Habitat ecology

Estuarine, generally in middle and upper reaches as far as upstream limit of tidal influence, sometimes collected in marine bays. Substrates: fine to coarse particle size, including bedrock. Flow: 0–60 cm/s (Kneipp, 1979). Water clarity: low to fair, sometimes tannin-stained in sand dune areas. Water depth: 0.1–27.0 m. Recorded physicochemical tolerances: water temperature 19–40 °C (field, this study $n = 7$; Kneipp, 1979, $n > 100$), pH 6.5–8.0 (field, $n = 10$), DO_2 5.0–9.3 ppm (field, $n = 2$). Fringing vegetation: mangroves, rainforest, heathland, anthropogenically-disturbed areas.

Behaviour

Shelters underneath mangrove roots, fallen timber, overhanging banks, boulders, rock ledges or rocks.

Distribution

Northern Australia [type locality: Sydney] and questionably New Caledonia. *Australian distribution*: Cape Leveque Coast and Fitzroy R. basins, W.A.; Buckingham R. basin, N.T.; Endeavour R. basin, Qld to the Sydney Coast-Georges R. basin, N.S.W.

Systematic position

This species appears allied to *M. equidens* (Dana, 1852) and *M. idae* (Heller, 1862a, b), both of which occur in sympatry. *M. novaehollandiae* differs from *M. equidens* in the following features:

1. The rostrum is generally straight and deep with the dorsal teeth subequally spaced. In *M. equidens* the rostrum is usually sigmoidal or upturned, of normal depth, and with the dorsal teeth tending to be more closely spaced in the proximal third than in the distal third (apart from the subapical teeth).
2. The pappose setal pubescence on the fingers of developed male P2 is restricted to the cutting edges rather than completely covering both fingers.
3. Live specimens have faint transverse bands or blotches on the segments of P2 rather than dark irregular blotches.

From *M. idae*, the species can be separated using the following features:

1. In *M. novaehollandiae* the P2 carpus is always shorter than the chela whereas in *M. idae* it is about equal in females and undeveloped males and distinctly longer in developed males.
2. The pappose setal pubescence on the fingers of P2 of developed males is extensive on the dactylus but restricted to the cutting edge of the propodus in *M. idae*. In *M. novaehollandiae* the pappose setal pubescence is restricted to the cutting edges of both fingers.

The faint transverse bands or blotches on the segments of P2 in *M. novaehollandiae* also contrast with the live colouration of *M. idae* – irregular dark blotches or longitudinal dark bands on P2.

The Asian species, *M. nipponense* (De Haan, 1849) and *M. sintangense* (De Man, 1898), although showing overall resemblance to *M. novaehollandiae*, differ in the relative length of the fingers of the developed male P2. In *M. novaehollandiae* the fingers are much less than half the length of the manus whereas in the other two species the fingers are over half the length of the manus.

Vernacular names

New Holland river prawn.

Remarks

This species was originally described from Sydney by De Man (1908) who proposed the name *Palaemon* (*Eupalaemon*) *novae-hollandiae* if it should prove to be distinct from *Palaemon (Eupalaemon) danae* Heller (=*M. australe*). Holthuis (1950) discussed the differences between this species and Heller's *P. danae* and recognised *M. novaehollandiae* (De Man) as the earliest available name. The material at hand agrees closely with the description and figures of De Man (1908).

Boone's record from New Caledonia of *M. aemulum* (Nobili) does appear to be this species as noted by Holthuis (1950). As yet no further

material has been reported from New Caledonia to confirm its occurrence there.

The three specimens recorded from southwest India by Jayachandran & Joseph (1989) show a number of significant differences from material I have examined and De Man's original description. The rostrum figured by Jayachandran & Joseph has a slightly sigmoidal dorsal carina and appears too slender for *M. novaehollandiae*. In Jayachandran and Joseph's species there are also three postorbital teeth. Although De Man's description mentions three rostral teeth on the carapace, his type figure shows only two teeth clearly behind the orbit. This is consistent in all the Australian material I have examined. The second pereiopods also appear to be far too stout, with the manus swollen, rather than elongated and cylindrical. The fingers are also too short and unlike developed males of *M. novaehollandiae*, the carapace and abdomen are described as glabrous by Jayachandran & Joseph. Their species does not resemble any previously described Indo-West Pacific species and is probably new to science.

This is one of the more easily recognised Australian species distinguished by its unusually long, slender second pereiopods and relatively straight, deep rostrum. It is very common in brackish waters from Sydney to Cooktown on the eastern coast. Across northern Australia the species is much rarer. Presently there are only three isolated records, two from the Kimberley Coast and the other from Elcho Island in the northeastern Northern Territory. The relative rarity of the species across the northern monsoonal tropics is somewhat puzzling. Perhaps it can partly be explained by the lengthy dry season of the region when most estuarine systems become marine intrusions and unsuitable for species preferring brackish water.

Macrobrachium equidens (Dana, 1852) (Figs 8, 9 36G)

Palaemon equidens Dana, 1852, p. 26. 1855, p. 12, pl. 39, fig. 2.

Palaemon equidens (*aequidens*) – Von Martens, 1868, p. 40.

Palaemon (*Eupalaemon*) *sundaicus*? – De Man, 1892, p. 437, pl. 26 fig. 35.

Palaemon (*Eupalaemon*) *sundaicus* – De Man, 1897, p. 779; 1898, p. 708, pl. 37 figs 70m, n, 71 (not Heller, 1862a).

Palaemon sundaicus bataviana – De Man, 1897, p. 784.

Palaemon (*Eupalaemon*) *sundaicus* var. – De Man, 1898, p. 72, pl. 37, figs 70o, 72.

Palaemon (*Eupalaemon*) *sundaicus brachydactyla* – Nobili, 1899, p. 238.

Palaemon sundaicus De Mani – Nobili, 1899, p. 239.

Palaemon (*Eupalaemon*) *acanthosoma* – Nobili, 1899, p. 242. De Man, 1915, p. 427, pl. 29 figs 10, 11.

Palaemon (*Eupalaemon*) *nasutus* Nobili, 1903, p. 9, text figure.

Palaemon sundaicus – Cowles, 1914, p. 355, pl. 2 fig. 3.

Macrobrachium equidens – Maki & Tsuchiya, 1923, p. 62, pl. 6 fig. 1 (may be young of *M. nipponense*, cf. Holthuis, 1950). Holthuis, 1950 (in part), pp. 14, 162–171. 1970, pp. 90–91. 1980, p. 90. Maccagno & Cucchiari, 1957, pp. 279 (key), 303–306, fig. 27. Johnson, 1973, pp. 283–285. Choy, 1984, p. 271. Liu et al., 1990, pp. 103 (key), 110–111, fig. 8. Bruce & Coombes, 1997, p. 302. Shy & Yu, 1998, pp. 21–22. Yeo et al., 1999, p. 226.

Palaemon nasutus – Nouvel, 1932, p. 409.

Palaemon sulcatus – Henderson and Matthai, 1910, p. 289, pl. 16 fig. 3.

Macrobrachium australiense – Holthuis, 1950, p. 175 (in part; specimen from Sydney?).

not *Macrobrachium equidens* – Kamita, 1972, p. 59, figs 1–3. Kim, 1977, pp. 226–230, text-figures 84, pp. 87–88, pls 21, 22, fig. 37 (=*M. koreanum* Kwon & Han, 1984).

(?) *Palaemon* n. sp? – De Man, 1888, pp. 711–714, fig. 3.

(?) *Macrobrachium sundaicus* – Maki & Tsuchiya, 1923, p. 57, pl. 2 fig. 2 (may be young of *M. nipponense*, cf. Holthuis, 1950).

(?) *Macrobrachium danae*: Riek, 1951, p. 360 (in part, not Heller, 1865).

Material examined

Northern Drainage Region. Fitzroy R Basin: WAM C21472, Derby, King Sound; WAM C11164, Derby jetty; WAM C21470, Doctors Ck near Derby, King Sound; *Prince Regent R Basin*: WAM

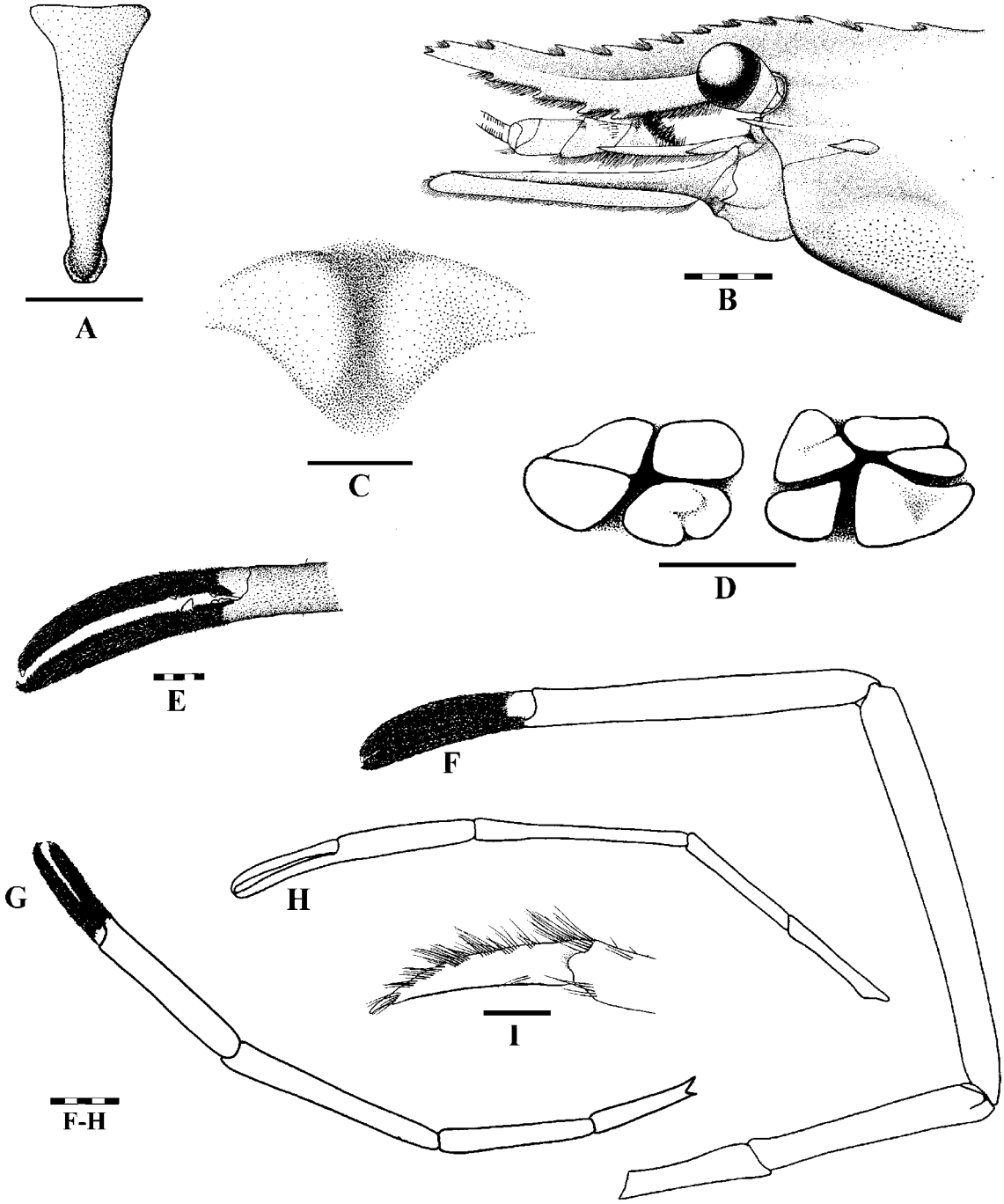

Figure 8. *Macrobrachium equidens* (Dana, 1852). (A) QM W5657, male 25.5 mm CL, ventral view of inter-uropodal sclerite, (B) QM W6674, male 27.2 mm CL, anterior cephalothorax, (C) QM W16403, male 21.8 mm CL, epistome, (D) crowns of left and right mandibular molar processes (setae omitted) of same, (E) QM W6674, male 27.2 mm CL, mesial view of fingers and distal manus of fully developed right chela, (F) fully developed right second cheliped (protective setation omitted), (G) QM W18135, male 16.7 mm CL, undeveloped left second cheliped (protective setation omitted), (H) QM W16750, female 20.0 mm CL, right second cheliped (protective setation omitted), (I) QM W15669, male 17.8 mm CL, dactylus and distal propodus of third pereiopod. Solid scale bars and divisions on divided scale bars 1 mm.

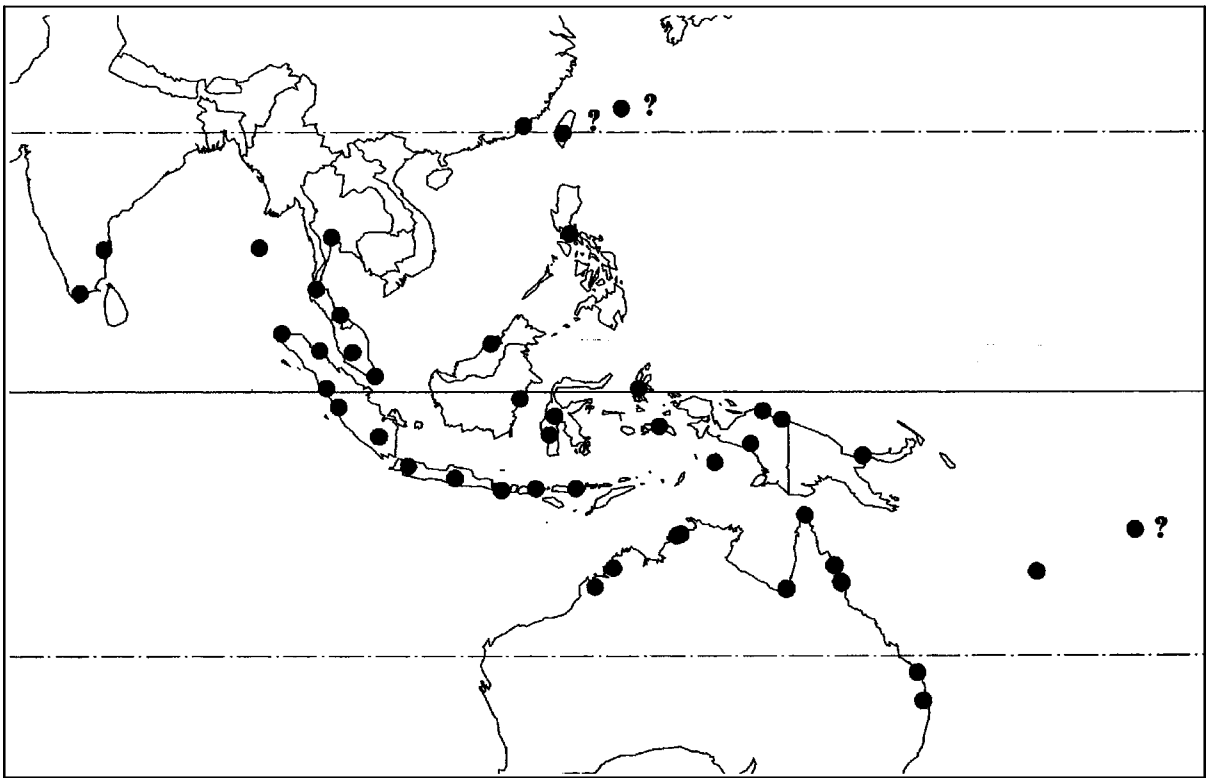

Figure 9. Distribution of *Macrobrachium equidens* (Dana, 1852).

C21468, King Cascades, Prince Regent R.; *Finniss R Basin*: QM W16548, Darwin R. near Cox Peninsula Rd bridge; NTM Cr007274, Mickett Ck; NTM Cr007274, King Ck mouth; NTM Cr002002, Leaders Ck near Gunn Pt; *Adelaide R Basin*: NTM Cr005853, Adelaide R., Arnhem Hwy bridge; QM W20940, Adelaide R. near Arnhem Hwy crossing; *Norman R Basin*: QM W17146, Norman R., 1 km upstream of Karumba; QM W8610, Norman R., Karumba; *Inshore Marine*: NTM Cr007273, Camerons Beach; NTM Cr007392, Chambers Bay; NTM Cr007272, Shoal Bay, King Ck area; WAM C11525, Gulf of Carpentaria, off Bynoe R.

Eastern Drainage Region. *Jacky Jacky Ck Basin*: QM W16750, Fishbone Ck near Jacky Jacky boat ramp; *Endeavour R Basin*: QM W19654, Endeavour R., 19 km NW Cooktown; QM W18135, Endeavour R., Endeavour Bridge near Cooktown; QM W5428, Endeavour R., Airport Crossing near Cooktown; *Barron R Basin*: QM W19233, Barron R., Kamerunga Bridge; *Mulgrave-Russell Rivers Basin*: QM W7888, Trinity Inlet, Cairns; QM W19940, Edmonton, downstream of junction of Wright and Stony Creeks, Page Rd; *Johnstone R Basin*: QM W22008, Unnamed creek near Innisfail; QM W21997, Johnstone R. at hospital bridge, Innisfail; *Ross R Basin*: AM P26622, north side of Cape Pallarenda; *Boyne R Basin*: NTM Cr007271, Gladstone; *Burrum R Basin*: QM W20024, Elliott R; *Brisbane R Basin*: QM W5657, Brisbane R.; QM W16403, Brisbane R., Norman Ck mouth; QM W6674, Brisbane R., between Victoria and Story Bridges; QM W15669, Norman Ck, Wynnum Rd bridge, Norman Park; *Inshore Marine*: AM P13181, Princess Charlotte Bay.

Uncertain locality: NNM, Sydney?, leg. R. Schütte (labelled '*Palaemon ruber* Hess var. digitis inermatis. type.')

Diagnosis

Rostrum. Medium length in fully developed males, developmental range 0.7–1.1 CL; moderately deep

(maximum depth slightly more than dorsoventral diameter of eye); dorsal carina sinuous or upturned, dentate along entire length, teeth tending to be more closely spaced proximally above orbit than distally, 9–15 teeth, 2–4 completely postorbital, all teeth immoveable in fully developed males; ventral carina dentate, 4–7 teeth, first tooth located in proximal half or at about mid-length.

General cephalon. Ocular cornea large, well-pigmented, accessory pigment spot present. Inferior orbit moderately produced, angular, postantennular carapace margin concave. Bec ocellaire strongly developed. Scaphocerite elongated, length greater than three times maximum breadth; lamina distinctly tapering from broadest point to anterior margin, anterior margin produced forward at inner angle. Epistome completely divided into two lobes, lobes rounded.

Mouthparts. Third maxilliped terminal segment clearly shorter than penultimate segment; exopod about equal in length to ischiomerus. Mandibular molar process crowns as figured (Fig. 8D).

Second chelipeds (fully developed male). Larger and more developed than female P2; isomorphic; long, merus reaching distal end of scaphocerite; bearing simple, protective and pappose setae; base of fingers, manus and proximal segments with abundant erect mamilliform protective setae, setae tending to be arranged in longitudinal rows, smaller and more closely spaced on inferior surfaces of carpus and propodus; pappose setae forming thick pubescence over fingers; simple setae scattered on manus and carpus, a few tufts on distal fingers; fingers more or less touching along their length; pollex elongated, basal breadth about equal to basal breadth of dactylus, uncinate at tip, proximal cutting edge with dentate ridge followed by distinct gap then large tooth, distally entire; dactylus elongated, uncinate at tip, proximal cutting edge with two large teeth, the first opposing ridge of teeth on pollex, the second slightly advanced of large tooth on pollex, distally entire; manus subcylindrical, slightly narrowed subdistally, maximum breadth *c*. equal to maximum merus breadth, much longer than dactylus; carpus clearly shorter than chela, tapered; merus much shorter than carpus, tapered; ischium with deep groove on superior and inferior faces, compressed, narrowed near mid-length.

Third pereiopods (fully developed male). Long, propodus reaching distal end of scaphocerite; all segments except dactylus and distal propodus covered in spinuliform protective setae; dactylus elongated, length more than four times basal breadth, ventral carina well developed; unguis poorly developed, less than one fifth length of remainder of dactylus.

Thoracic sternum. T4 with well-developed median process, postcoxal flanges situated posterior to and distinct from median process. Fully developed male T8 with anterolateral lobes widely separated posteromedially, median process present posteriorly, process rounded or carinate, spinate in young males.

Abdomen. Inter-uropodal sclerite without preanal carina. Distolateral process on uropodal exopod with accessory spiniform seta mesially.

Body setation (fully developed male). Protective setation present on carapace and abdomen, carapace with scattered spinuliform protective setae, most abundant anterolaterally, abdomen with spinuliform and mamilliform protective setae on lower pleura, tergite 6, uropods and telson.

Colour

Antennal and outer antennular flagella translucent olive grey, inner antennular flagella dark olive brown, scaphocerites translucent olive grey, specked with olive brown. Rostrum translucent olive grey with red brown to olive brown specks, specking most developed along lateral carina. Ocular peduncles cream with specks of olive to red brown. Carapace cream, specked irregularly with olive to rusty brown, specks tending to be arranged in well spaced clumps laterally, in young specimens forming a few irregular stripes. Abdomen cream, specked with olive to rusty brown, uropods translucent olive to blue grey with plumose setae red brown.

Second pereiopods marbled with large areas of irregular dark olive brown blotches merging into smaller areas of red brown, drab grey and light yellow brown, ischium and merus blue grey and light cream. Fingers dark olive brown with lighter coloured tips varying from drab grey to white.

P3–5 marbled with dark olive brown and red brown distally, dactylus grey, proximal segments with indistinct bands of blue grey, red brown and cream.

Undeveloped ova olive.

Life cycle

Euryhaline, widespread throughout tidal reach, sometimes upstream as far as limit of tidal influence, 0–33 ppt salinity, ovigerous females occurring in inshore marine areas; eggs small and numerous, c. 1000–6000 per brood, maximum length of developed ova 0.7 mm; larval development extended, 10 planktonic stages, 36–53 days to metamorphosis at 32.9 ppt salinity/26–29.5 °C and 50–62 days at same salinity/25 °C (Nguyen Ngoc Ho, 1976).

Size

Medium-sized species. Maximum size of developed male c. 30 mm CL, 115 mm TL. Maximum size of female 23 mm CL, c. 90 mm TL, minimum size of ovigerous female, 14 mm CL.

Habitat ecology

Estuarine, generally in middle and lower reaches but occasionally upstream to limit of tidal influence. Ovigerous females also commonly trawled in marine inlets and bays. Substrates: Fine to coarse particle size, including bedrock. Flow: tidal. Water clarity: low to fair. Water depth: 0.1–18.0 m. Recorded physico-chemical tolerances: pH 7 (field, $n = 2$). Fringing vegetation: mangroves, rainforest or anthropogenically disturbed.

Behaviour

Shelters underneath mangrove roots, fallen timber, overhanging banks, boulders, rock ledges or rocks. Large males secretive, difficult to trap.

Distribution

Wide-ranging Indo-West Pacific from Travancore, India to southern China and Fiji [type locality: Singapore]. Apparently introduced to West Africa (Powell, 1987). *Australian distribution:* Fitzroy R. basin, W.A. to the Brisbane R. basin, Qld.

Systematic position

Macrobrachium equidens (Dana, 1852) appears closely allied to *M. novaehollandiae* (De Man, 1908) and *M. idae* (Heller, 1862a, b). The differences between *M. equidens* and *M. novaehollandiae* have been discussed under the latter species.

From *M. idae*, it differs in having the P2 carpus always shorter than the chela (like *M. novaehollandiae*). In *M. idae* the carpus is about equal to the chela in length in females and undeveloped males and distinctly longer in developed males. The pappose setal pubescence on the fingers of P2 of developed males also covers both fingers in *M. equidens* whereas in *M. idae* it is extensive on the dactylus but restricted to the cutting edge of the propodus only.

Young specimens of *M. rosenbergii* have a similar long, sigmoidal rostrum but differ in having the scaphocerite strongly produced forward at or near the mid-line of the anterior margin rather than produced forward at the inner angle. The pubescence on the fingers of the developed male P2 is also restricted to the proximal two-thirds of the dactylus in that species.

Although the developed male P2 of *M. mammillodactylus* differs markedly in lacking a pappose setal pubescence on the fingers, young specimens may appear very similar to *M. equidens* (as noted by Holthuis, 1950 and Chace & Bruce, 1993). However I have not found the features used by Holthuis (1950), i.e. the rostral formula and the shape of the outer margin of the scaphocerite to be totally reliable for distinguishing the two species. The shape of the epistome lobes is an easier character to use – in *M. equidens* the lobes are rounded whereas in *M. mammillodactylus* they are bluntly carinate. Features of the developed male P2 can also be used with caution:

1. The protective setation is less developed and individual setae hard to see in *M. mammillodactylus* whereas in *M. equidens* they are obvious from an early stage of development.
2. In *M. mammillodactylus* the fingers are much more slender and curved, and have an obvious gape which develops quickly.

Vernacular names

Rough river prawn (FAO).

Remarks

Although only recently recorded from Australia (Bruce & Coombes, 1997; based on material I identified in the NTM in 1990), this is a ubiquitous species in estuaries across the northern monsoonal tropics. On the east coast south of Townsville, *M. novaehollandiae* is the dominant estuarine species and *M. equidens* is largely confined to the lower estuarine reaches.

Australian specimens agree closely with previous illustrations and diagnoses (De Man, 1898; Cowles, 1914; Holthuis, 1950; Johnson, 1973; Liu et al.,1990; Chace & Bruce, 1993). Holthuis (1950) gives a detailed account of the nomenclatural history of the species which was better known in the early literature as *Palaemon sundaicus*. Johnson (1973) considered that all east African and Madagascan records previously assigned to *M. equidens* by Holthuis (1950) are more likely *M. rude* (Heller, 1862b) and is followed here.

The species provisionally assigned to *M. australiense* by Holthuis (1950) and originally reported by De Man (1898, p.711; from the collection of the Göttingen Museum) as *Palaemon* n. sp? from Sydney, N.S.W. is possibly this species and differs from *M. australiense* in having the merus of the second pereiopods clearly shorter than the carpus (McNeill, 1929). Similarly, the specimen reported by Holthuis (1950) from Sydney as *M. australiense*, and labelled '*Palaemon ruber* Hess var. digitis inermatis type', is in my opinion *M. equidens*. It agrees more closely with the diagnosis given above i.e. angular inferior orbit; no trace of a pre-anal carina on the interuropodal sclerite; slightly sigmoidal rostrum; prominent protective setae on P2; and larger body size. As with most of Schütte's material located in European museums, the locality 'Sydney' must be accepted with some reserve.

It is likely that the material reported by Riek (1951) under the name *Macrobrachium danae* (Heller) is at least partly this species. Riek states that the species (*M. danae*) 'is restricted almost entirely to salt water'. Since he distinguishes it from *M. novaehollandiae*, the only other possibility from estuarine/inshore marine areas in subtropical eastern Australia is *M. equidens*. However, he also noted that it 'may enter small freshwater springs and swamps at the shore-line'. As far as I know the only species in the region which is capable of utilising these habitats is *M. tolmerum* Riek. *M. danae* Riek may therefore be a combination of both species. Unfortunately, no precise localities were given and I have not been able to find registered material in Australian museum collections identified as *M. danae* by Riek.

I agree with Holthuis (1950) that *M. danae* Heller is a likely junior synonym of *M. australe* Guérin-Méneville. However, Heller's type locality 'Sydney' is probably incorrect. So far, I have no other records of *M. australe* from Australia despite the very large collection of Australian material at my disposal. Sydney lies at the southern coastal limit of the genus in Australia and experiences a subtropical climate. It is far more likely that the species will be found in the wet tropical region of northeast Queensland where species diversity is much higher.

Macrobrachium idae (Heller, 1862) (Figs 10, 11, 36F)

Restricted synonymy

Palaemon Idae Heller, 1862a, p. 416, pl. 2, figs 40, 41.

Macrobrachium palawanensis – Johnson, 1962, pp. 307–310, fig. 1; 1973, pp. 274, 282.

Macrobrachium idae – Holthuis, 1950, pp. 15, 106 (key), 142–146, fig. 33 (complete earlier literature). 1980, pp. 92–93. Maccagno & Cucchiari, 1957, pp. 277 (key), 316–318, fig. 31. Johnson, 1963, pp. 5–6 (? in part). Kensley, 1972, p. 42, fig. 19D. Chace & Bruce, 1993, pp. 21 (key), 27–28, fig. 6. Yeo et al., 1999, p. 226. Short, 2000, p. 64. Cai & Ng, 2001, pp. 678–683 figs, 12, 13. Wowor & Choy, 2001, pp. 283–284.

(?) *Macrobrachium idella* – Jalihal et al., 1988, p. 51–59, figs 14–16 (in part).

Material examined

Eastern Drainage Region. *Jeannie R Basin*: QM W18233, McIvor R., Isabella-McIvor Rd crossing; *Endeavour R Basin*: QM W18137, Endeavour R.,

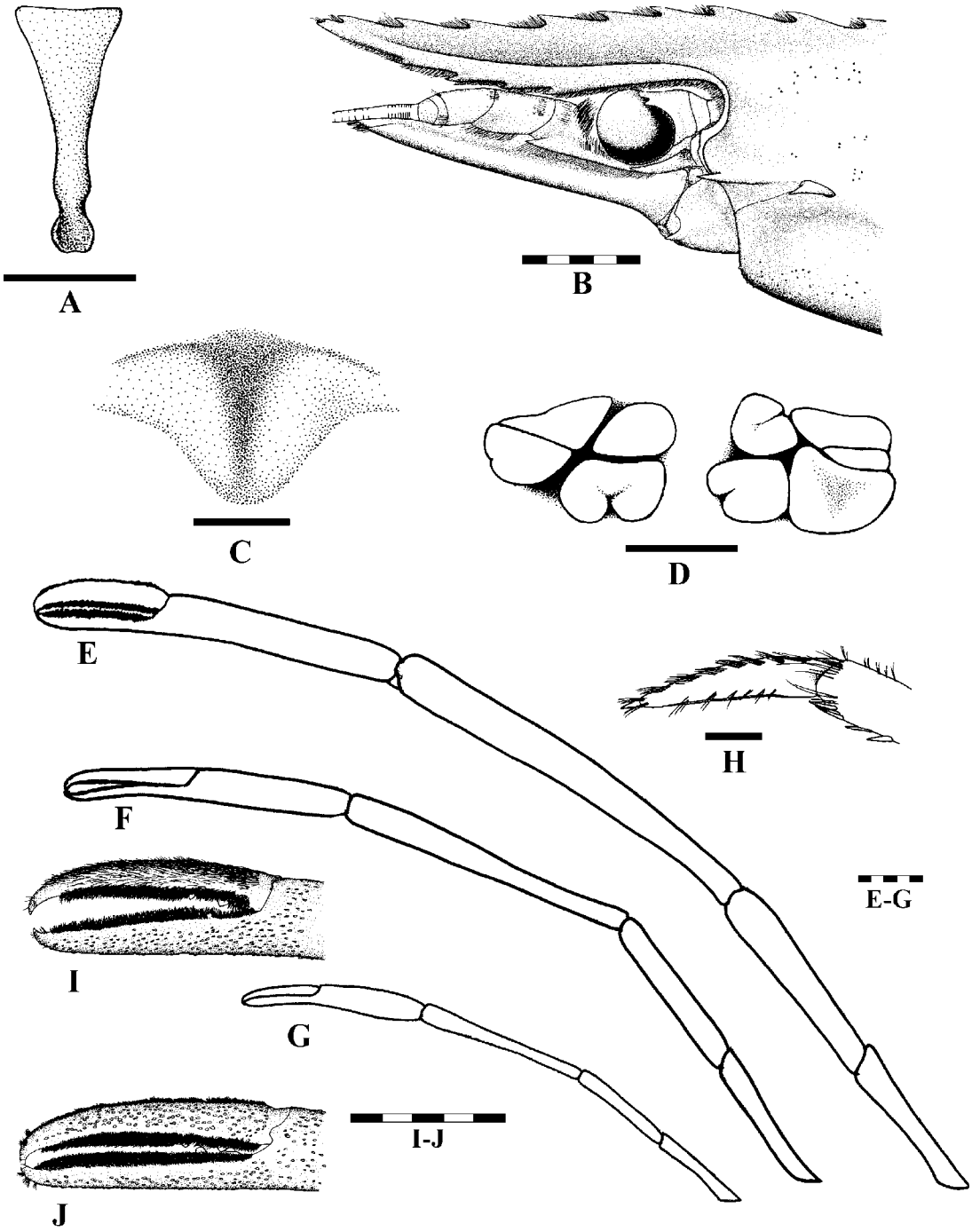

Figure 10. Macrobrachium idae (Heller, 1862). (A) QM W19616, male 21.8 mm CL, ventral view of inter-uropodal sclerite, (B) anterior cephalothorax of same, (C) epistome of same, (D) crowns of left and right mandibular molar processes (setae omitted) of same, (E) fully developed right second cheliped (protective setation omitted), (F) QM W18233, male 23.4 mm CL, undeveloped right second cheliped (protective setation omitted), (G) QM W22058, female 16.7 mm CL, right second cheliped (protective setation omitted), (H) QM W18233, male 26.5 mm, dactylus and distal propodus of right third pereiopod, (I) QM W19616, male 21.8 mm CL, lateral view of fingers and distal manus of fully developed right cheliped, (J) mesial view of same. Solid scale bars and divisions on divided scale bars 1 mm.

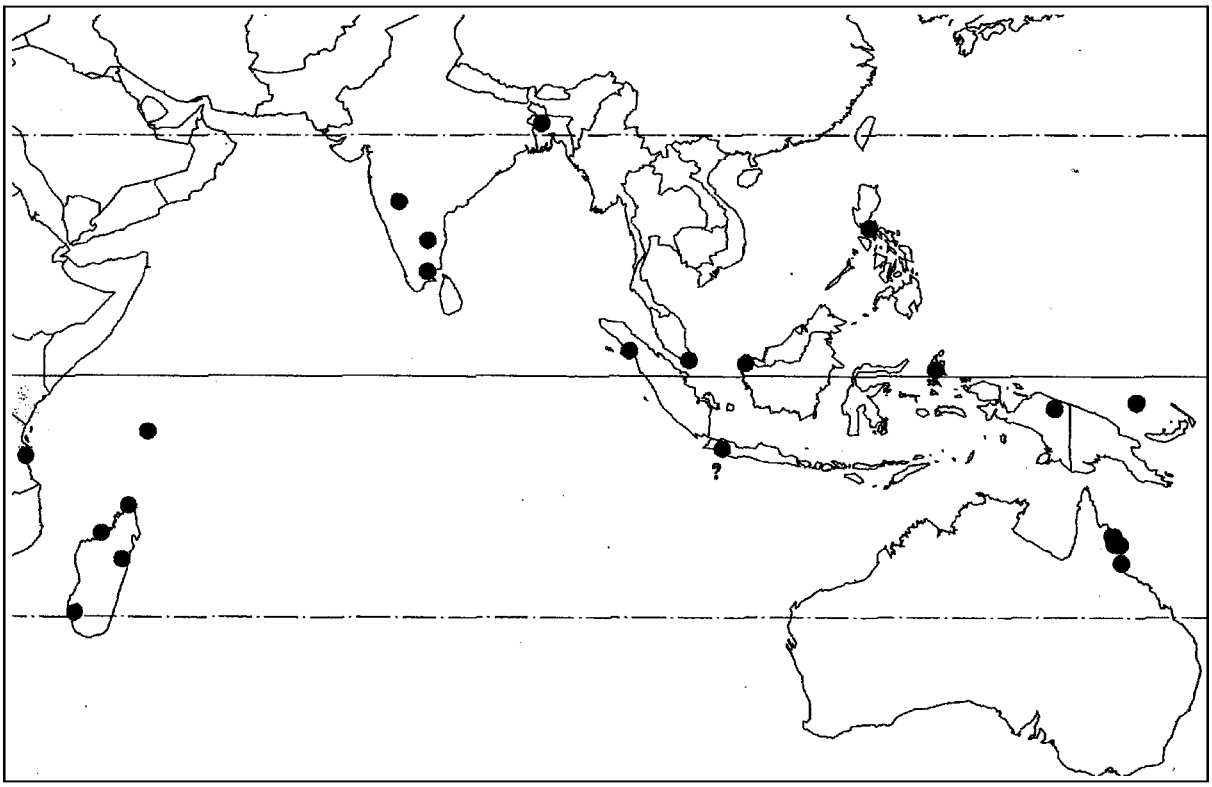

Figure 11. Distribution of *Macrobrachium idae* (Heller, 1862).

Jensens Crossing; QM W5421, Endeavour R., 19 km NW of Cooktown; QM W22042, Endeavour R. below first falls; QM W5422, Barretts Lagoon near Cooktown; *Daintree R Basin*: QM W12604, Daintree R., in canal work near ferry crossing; QM W19616, Daintree R., 2 km upstream of Daintree; *Barron R Basin*: QM W22216, Freshwater Ck, Cairns; *Mulgrave-Russell Rivers Basin*: QM W22058, Gordon Ck, Woree, c. 200 m above limit of tidal influence; *Johnstone R Basin*: QM W22006, Unnamed creek near Innisfail; *Murray R Basin*: QM W14233, Murray R., Tates Landing; *Herbert R - Palm Islands Basin*: QM W22061, Herbert R. at John Row bridge.

Non-Australian material: QM W24108, Kamora R. estuary near Timika, southern Irian Jaya.

Diagnosis

Rostrum. Medium length in fully developed males, developmental range 0.65–1.3 CL; moderately deep at mid-length (maximum depth slightly less than to slightly greater than dorsoventral diameter of cornea) but generally slender in distal third; dorsal carina sinuous, upturned, convex or straight, dentate, teeth often irregularly spaced, 8–12 teeth, 2–3 completely postorbital, all teeth immoveable in fully developed males; ventral carina dentate, 3–6 teeth, first tooth generally located in proximal half.

General cephalon. Ocular cornea large, well-pigmented, accessory pigment spot present. Inferior orbit moderately produced, angular, postantennular carapace margin concave, rarely straight. Bec ocellaire strongly developed. Scaphocerite elongated, length three times maximum breadth, lamina distinctly tapering from broadest point to anterior margin, anterior margin produced forward at inner angle. Epistome completely divided into two lobes, lobes rounded.

Mouthparts. Third maxilliped terminal segment clearly shorter than penultimate segment; exopod about equal in length to ischiomerus. Mandibular molar process crowns as figured (Fig. 10D).

Second cheliped (fully developed male). Isomorphic; long, merus reaching distal end of scaphocerite; bearing protective and pappose setae; protective setae abundant, mostly mamilliform (slightly flattened), tending to be more squamiform on superior manus; pappose setal pubescence extensive on lateral dactylus, otherwise largely restricted to cutting edges; fingers with weak gape; pollex moderately slender, evenly tapered, not noticeably broadened basally, about equal in breadth to basal dactylus, uncinate at tip, proximal cutting edge with dentate ridge followed by distinct gap then large tooth, distally entire; dactylus moderately slender, uncinate at tip, proximal cutting edge with two large teeth, the first opposing ridge of teeth on pollex, the second slightly advanced of large tooth on pollex, distally entire; manus subcylindrical, slightly expanded distally, maximum breadth less than or c. equal to maximum merus breadth, much longer than dactylus; carpus slightly longer than chela, elongated, tapered, slender until about mid-length, abruptly expanded distally; merus much shorter than carpus, tapered; ischium with well developed longitudinal groove on superior and inferior faces, narrowed at about mid-length.

Third pereiopods (fully developed male). Long, propodus reaching distal end of scaphocerite; protective setation absent; dactylus elongated, length more than four times basal breadth, ventral carina well developed; unguis poorly developed, one fifth or less of remainder of dactylus.

Thoracic sternum. T4 with well-developed median process, postcoxal flanges situated posterior to and distinct from median process. Fully developed male T8 with anterolateral lobes widely separated posteromedially, median process present posteriorly, process rounded, carinate or spinate.

Abdomen. Inter-uropodal sclerite without preanal carina. Distolateral process on uropodal exopod with accessory spiniform seta mesially.

Body setation (fully developed male). Protective setation present on anterior carapace and lower pleura and telson of abdomen, protective setae slightly flattened, mamilliform.

Colour

Antennal flagella banded with alternating olive brown and light orange brown bands, peduncles olive brown, scaphocerites cream to olive grey with olive brown to blue grey specks.

Rostrum translucent olive grey specked with olive brown to olive grey. Ocular peduncles olive grey with dark olive brown blotches. Carapace dirty olive grey with large irregular dark olive brown blotches. Abdomen dirty olive grey to olive yellow specked with olive brown, condyles dark olive brown, tailfan also with a few dark blotches, fringing plumose setae orange brown.

Second pereiopods uniformly dark grey brown with light coloured finger tips in adults, light olive yellow with orange brown markings in young specimens. Propodi and dactyli of ambulatory pereiopods of adults with alternating dark olive brown and light orange brown bands; merus, carpus and ischium with less distinct dark olive brown and orange brown bands, first chelipeds and ambulatory legs of young specimens light orange brown with dark orange brown specks.

Life cycle

Euryhaline, 0–33 ppt salinity, amphidromous, adults common in lowland fresh waters; eggs small and numerous, c. 500–3000 per brood, maximum length of developed ova, 0.6 mm; larval development extended, 12 planktonic stages, development initially in 32.1–32.9 ppt salinity but only completed in 90% seawater (Nguyen Ngoc Ho, 1976; as *Macrobrachium* sp.)

Size

Medium-sized species. Maximum recorded size of developed male 27 mm CL (this study), 110 mm TL (Holthuis, 1980). Maximum size of female 18.5 mm CL (this study), minimum size of ovigerous female, 10.5 mm CL (this study).

Habitat ecology

Common in lowland coastal areas (<40 m elevation), including estuaries, freshwater waterholes and billabongs. Substrates: fine to coarse, possibly with a preference for fine substrates. Flow: low to moderate flow. Water clarity: low to high. Water

depth: 0.3–3.0 m. Recorded physico-chemical tolerances: hardness <20–50 ppm (field, $n = 6$), DO_2 0.5–11.5 ppm (field, $n = 6$), water temperature 20–25 °C (field, $n = 5$), pH 6.25–7.0 (field, $n = 6$). Fringing vegetation: mangroves or rainforest.

Behaviour

This species may be piscivorous in the wild as it is very adept at catching fish in an aquarium – the chelipeds are raised with pincers open and held motionless until a passing fish comes within striking distance.

Distribution

Wide-ranging Indo-West Pacific: east Africa to the Philippines, New Guinea and the Admiralty Islands [type locality: Borneo]. *Australian distribution:* Northeast Qld; Jeannie R. basin to Herbert R. basin.

Systematic position

This species appears to be closely allied to *M. equidens*, *M. novaehollandiae* and *M. mammillodactylus*. It differs from all three species in having the chela of P2 clearly shorter than the carpus in developed males (Fig. 10E) and equal to or slightly longer than carpus in females and undeveloped males (Fig. 10F and G). In the other three species the chela is always distinctly longer than the carpus. Another distinctive feature of the developed male P2 of *M. idae* is the setation pattern on the lateral fingers. The dactylus is largely covered by a well-developed pappose setal pubescence whereas on the propodus the pubescence is restricted to the cutting edge. In *M. mammillodactylus* there is no setal pubescence on the chela, in *M. equidens* both fingers are completely covered, and in *M. novaehollandiae* setae are largely restricted to the cutting edge on both fingers.

A close relationship with *M. idella* (Hilgendorf, 1898) has also been suggested by previous authors (Holthuis, 1950; Jalihal et al., 1988). Unfortunately, the taxonomy of *M. idella* is unclear at present (see remarks below). Based on the original descriptions of both species there does appear to be a significant difference in the size of the eggs (0.6 mm maximum length in *M. idae* vs. 1.25 mm in *M. idella*) and the rostral formula (8–12 dorsal teeth in *M. idae* vs. 12–17 (rarely 11) in *M. idella*).

This species was based on a syntype series from Borneo. Cai & Ng (2001) erected a lectotype from Heller's syntypes and synonymised *M. palawanensis* Johnson, 1962.

Vernacular names

Ida's river prawn; Orana river prawn (FAO); Orana, Camaron (Madagascar; cf. Holthuis, 1980).

Remarks

Cai & Ng (2001) erected a lectotype for the species from Heller's syntype series in the Naturhistorisches Museum, Wien. The present material agrees closely with their illustrations of the lectotype and with the descriptions and figures of previous authors (Heller, 1862a; De Man, 1897; Holthuis, 1950).

Johnson (1963) described the largest of his series of specimens from Singapore as possessing a row of tubercles (= bulliform protective setae) on either side of the cutting edge of each finger of the second pereiopods. Although the largest specimens I have examined during this study from Australia and southern Irian Jaya are of similar size to Johnson's specimen and appear to have fully developed chelipeds they do not show this character. It is possible that Johnson's specimen was *M. mammillodactylus* rather than this species.

The relationship between *M. idae* and *M. idella* (Hilgendorf, 1898) needs to be more clearly defined. Jalihal et al. (1988) reported *M. idella* from India but the recorded egg size differs markedly from Hilgendorf's original description. According to Jalihal et al. (1988) the eggs are small and have a maximum length of 0.62 mm whereas in Hilgendorf's original description the eggs are said to be moderately large at 1.25 mm. The egg size of Jalihal's species is closer to *M. idae*. Jalihal et al.

(1988) distinguished the two species on the number of dorsal rostral teeth although the rostral formulae of the two species overlap. The carpus of the second pereiopod was also said to be relatively longer in *M. idae*.

Australian records of *M. idae* are limited to northeast Queensland, although the species has a wide distribution in the Indo-West Pacific. Adults appear to prefer lowland fresh water around the upstream limit of tidal influence and low salinity estuarine waters.

Macrobrachium mammillodactylus (Thallwitz, 1892) (Figs 12, 13)

Palaemon idae mammillodactylus Thallwitz, 1892, p. 15.
Palaemon (Eupalaemon) Wolterstorffi – Nobili, 1900, p. 1.
Palaemon philippinensis – Cowles, 1914, p. 340, pl. 2 fig. 2.
Macrobrachium mammillodactylus – Holthuis, 1950, pp. 16, 106 (key), 148–150, fig. 34; 1980, pp. 99–100. Shy & Yu, 1998, p. 40.
(?) *Palaemon talaverae* – Blanco, 1939, p. 168, pl. 2.

Material examined

Eastern Drainage Region. Lockhardt R Basin: QM W7290, 1 imm., CL 10.2 mm, Line Hill, Iron Ra. QM W19656, 2 males, CL 10.9, 19.5 mm, 1 female, CL 20.0 mm, 4 imm., CL 7.9–10.2 mm, same locality; AM P19035, 1 male, CL 21.1 mm, Iron Ra., foothills of Mt Tozen; *Normanby R Basin*: QM W16639, 6 males, CL 15.4–28.1 mm, 1 female, CL 12.0 mm, 1 imm., CL 9.1 mm, Normanby R., Orange Plain Waterhole; *Endeavour R Basin*: QM W5419, 5 males, CL 10.0-21.4 mm, 1 female, CL 16.9 mm, Endeavour R., 19 km NW of Cooktown.

Non-Australian Material. Southern Irian Jaya: QM W24120, 105 unsexed, Kamora R. near Timika; QM W24118, 2 males, CL 21.8–24.0 mm, 3 females, CL 13.2–18.6 mm, 4 juveniles, Main Ajkwa R. near Timika; *Papua New Guinea*: QM W19998, 1 male, CL 23.1 mm, Suki Ck, upper Fly R. catchment.

Diagnosis

Rostrum. Short to medium length in fully developed males, developmental range 0.75–1.25 CL (this study), deep in proximal half (maximum depth clearly more than dorsoventral diameter of eye), abruptly tapered in distal half; dorsal carina generally straight with upturned tip, otherwise sinuous, upturned or straight, dentate along entire length, teeth tending to be more closely spaced in proximal half, 9–18 teeth, 2–3 completely postorbital, all teeth immoveable in fully developed males; ventral carina dentate, 2–6 teeth, first tooth generally located well within proximal half.

General cephalon. Ocular cornea large, well-pigmented, accessory pigment spot present. Inferior orbit moderately produced, angular, postantennular carapace margin concave. Bec ocellaire strongly developed. Scaphocerite stout, length less than 3 times maximum breadth, lamina distinctly tapering from broadest point to anterior margin, anterior margin produced forward at inner angle. Epistome completely divided into two lobes, lobes with blunt slightly-oblique longitudinal carinae.

Mouthparts. Third maxilliped terminal segment clearly shorter than penultimate segment; exopod about equal in length to ischiomerus. Mandibular molar process crowns as figured (Fig. 12D).

Second chelipeds. Isomorphic in shape and setation, subequal or equal in length; long, merus reaching distal end of scaphocerite; bearing protective and simple setae only; all segments except fingers with abundant short mamilliform protective setae, few and scattered on fingers; simple setae scattered on all segments except for few tufts on fingers; fingers with well developed gape in distal half, armed with three submedial rows of well-spaced heavily-tanned bulliform protective setae, a mesial and a lateral row near the cutting edge of dactylus and a mesial row near cutting edge of propodus; pollex elongated, not noticeably broadened basally, about equal in breadth to basal dactylus, uncinate at tip, proximal cutting edge with ridge of small teeth followed by distinct gap then large tooth, distally entire; dactylus elongated, uncinate at tip, proximally with two large teeth, the first opposing ridge of teeth on pollex, the second slightly advanced of large tooth on pollex, distally entire; manus subcylindrical, gen-

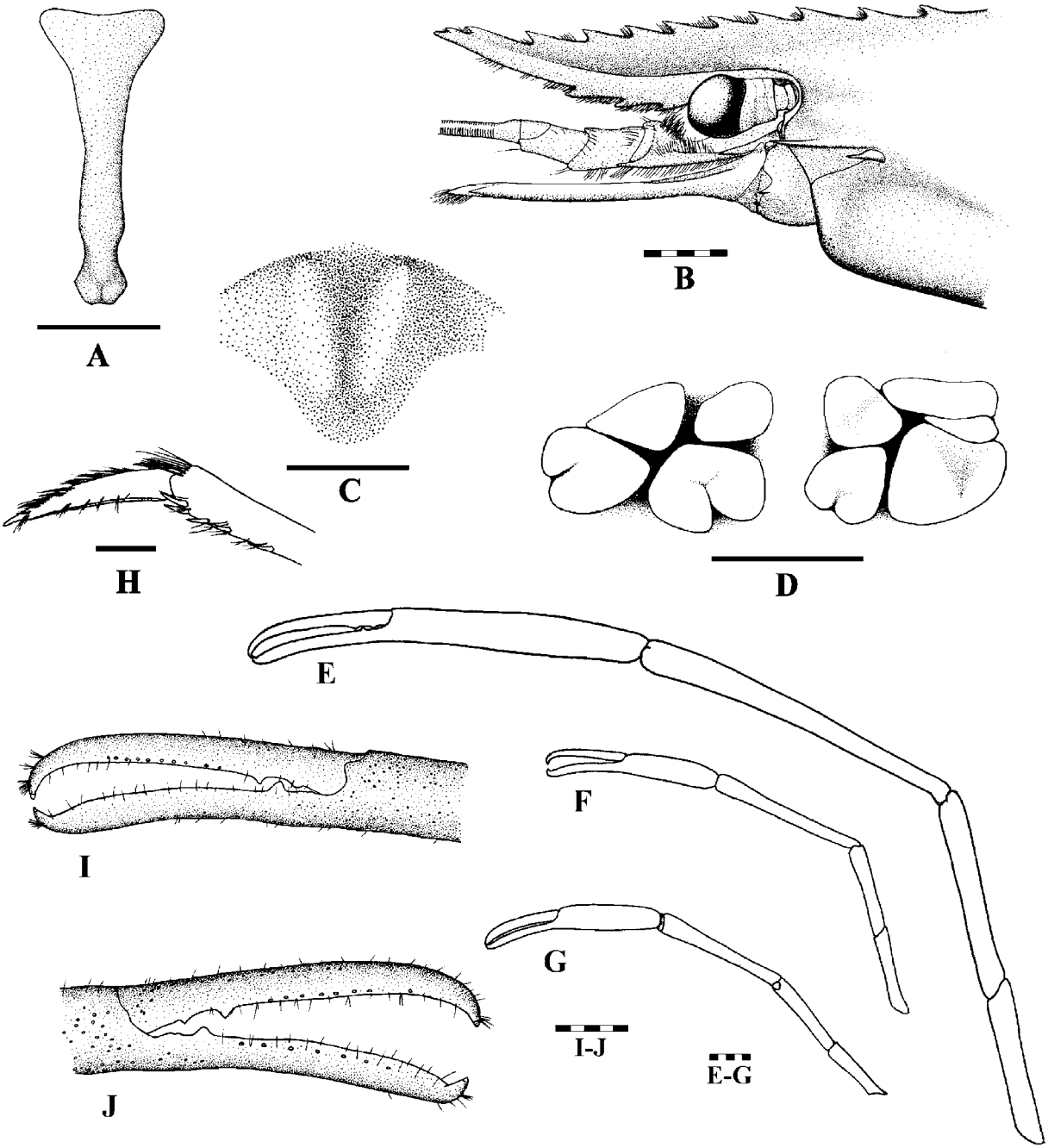

Figure 12. Macrobrachium mammillodactylus (Thallwitz, 1892). (A) QM W19656, female 20.0 mm CL, ventral view of inter-uropodal sclerite, (B) QM W16639, male 28.0 mm CL, anterior cephalothorax, (C) epistome of same, (D) crowns of left and right mandibular molar processes (setae omitted) of same, (E) developed right second cheliped (protective setation omitted), (F) QM W5419, male 21.7 mm CL, undeveloped right second cheliped (protective setation omitted) (G) QM W19656, female 20.0 mm CL, right second cheliped (protective setation omitted), (H) QM W5419, male 21.7 mm CL, dactylus and distal propodus of right third pereiopod, (I) QM W16639, male 28.0 mm CL, mesial view of fingers and distal manus of fully developed right cheliped, (J) lateral view of same. Solid scale bars and divisions on divided scale bars 1 mm.

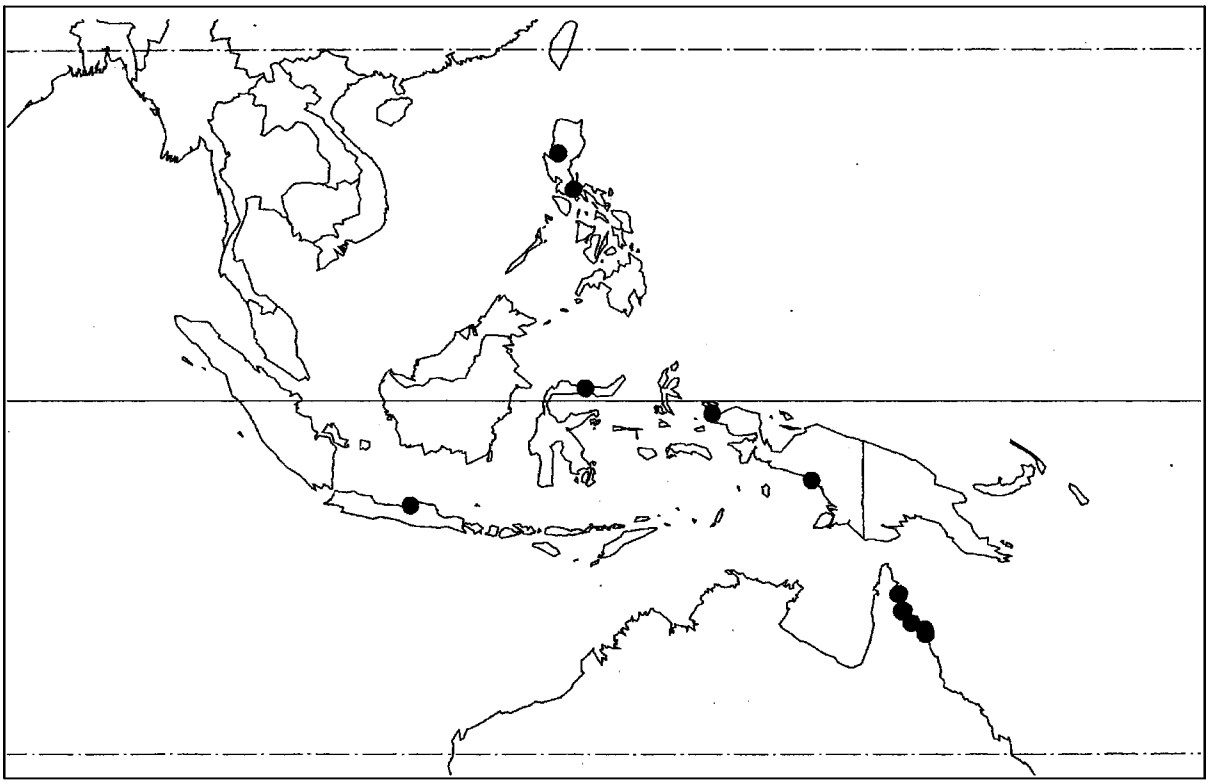

Figure 13. Distribution of *Macrobrachium mammillodactylus* (Thallwitz, 1892).

erally slightly inflated in middle third, much longer than dactylus; carpus clearly shorter than chela, elongated, tapered, often slightly inflated subdistally; merus much shorter than carpus, tapered; ischium with well developed median groove on superior face and less developed groove on inferior face, compressed, slightly narrowed at mid-length.

Third pereiopods (fully developed male). Long, propodus reaching distal end of scaphocerite; mamilliform protective setae abundant on all segments except dactylus; dactylus elongated, length over four times basal breadth, ventral carina well developed; unguis poorly developed, less than one fifth length of remainder of dactylus.

Thoracic sternum. T4 with well-developed median process, postcoxal flanges situated posterior to and distinct from median process. Fully developed male T8 with anterolateral lobes widely separated posteromedially, median process present posteriorly, process rounded or carinate, spinate in young males.

Abdomen. Inter-uropodal sclerite without preanal carina. Distolateral process on uropodal exopod with accessory spiniform seta mesially.

Body setation (fully developed male). Short mamilliform protective setation present on carapace and abdomen, on carapace mostly restricted to anterolateral regions, sometimes present on dorsum, on abdomen occurring on lower pleura, uropods and telson.

Colour

Not recorded in this study. Cowles (1914, fig. 2m) illustrated the characteristic chromatophore markings on the carapace of this species.

Life cycle

Euryhaline, amphidromous, adults predominantly in lowland fresh waters but extending into brackish water (Cowles, 1914); eggs small and numerous, c. 250–3000 per brood, maximum length of developed

ova 0.7 mm. Larval cycle unstudied, small egg size indicative of extended larval development.

Size

Large species. Maximum size of developed male, 137 mm TL (Holthuis, 1980). Maximum size of female 20 mm CL, 81 mm TL, minimum size of ovigerous female, 10 mm CL (this study).

Habitat ecology

A lowland, coastal species (<40 m elevation). Substrates: fine to coarse. Flow: zero to moderate flow. Water depth: 0.5–3.0 m. Water clarity:low to high, including tannin-stained water. Fringing vegetation: rainforest.

Distribution

Central Indo-West Pacific: southern China, the Philippines [type locality: Luzon], Indonesia, New Guinea. *Australian distribution*: Northeast Qld; Olive-Pascoe Rivers basin to Endeavour R. basin.

Systematic position

This species appears allied to *M. idae* (Heller, 1862a, b). The distinguishing features between *M. mammillodactylus* and *M. idae* have already been discussed above under *M. idae*. The distinctive submedial rows of bulliform protective setae (= tubercles of previous authors) on the cutting edges of the fingers of the developed male P2 also suggest a close relationship with *M. bullatum* Fincham, 1987, an endemic Australian species, and *M. minutum* (Roux, 1917) only known from northern New Guinea. These two species are much smaller in size (*M. minutum* to 47 mm TL and *M. bullatum* to 72 mm TL vs. 137 mm maximum TL for *M. mammillodactylus*) and have shorter third pereiopods – in developed males reaching the distal end of the scaphocerite by at most the base of the dactylus vs. the propodus reaching the distal end of the scaphocerite in *M. mammillodactylus*.

M. bullatum also differs in having moderately large ova (c. 1.4 mm maximum length vs. c. 0.7 mm maximum length in *M. mammillodactylus*) and second pereiopods of markedly dissimilar length (minor cheliped fails to reach distal end of manus of major cheliped). In *M. mammillodactylus* the second pereiopods are isomorphic.

Vernacular names

Knobtooth river prawn (FAO).

Remarks

This is the first record of *M. mammillodactylus* from Australia. Although the Australian material examined does not include a fully developed male, the largest males show the characteristic rows of bulliform protective setae (= tubercles of previous authors) submedially on the cutting edges of the fingers of P2. The shape of the second pereiopods and rostral formula of Australian material agree closely with previous description, illustrations and diagnoses. As described by Cowles (1914), rostral teeth on the carapace and near the tip of the rostrum tend to be more widely spaced than the teeth on the middle third of the rostrum.

Although the species has a wide distribution in the Central Indo-West Pacific, Australian records are so far limited to lowland fresh waters on eastern Cape York Peninsula as far south as the Endeavour R. near Cooktown.

Macrobrachium bullatum Fincham, 1987 (Figs 14, 15, 36B)

Macrobrachium bullatum Fincham, 1987, pp. 351–354, fig. 1.
(?) *Palaemon australis* – Roux, 1933, p. 344.

Material examined

Holotype
Northern Drainage Region. East Alligator R Basin: NTM Cr003097, 1 male, CL 17.1 mm, Magela Ck, 3/6/1984, H.E. Allison.

Paratypes
NTM Cr003085, 1 ovig. female, CL 13.8 mm, same locality.

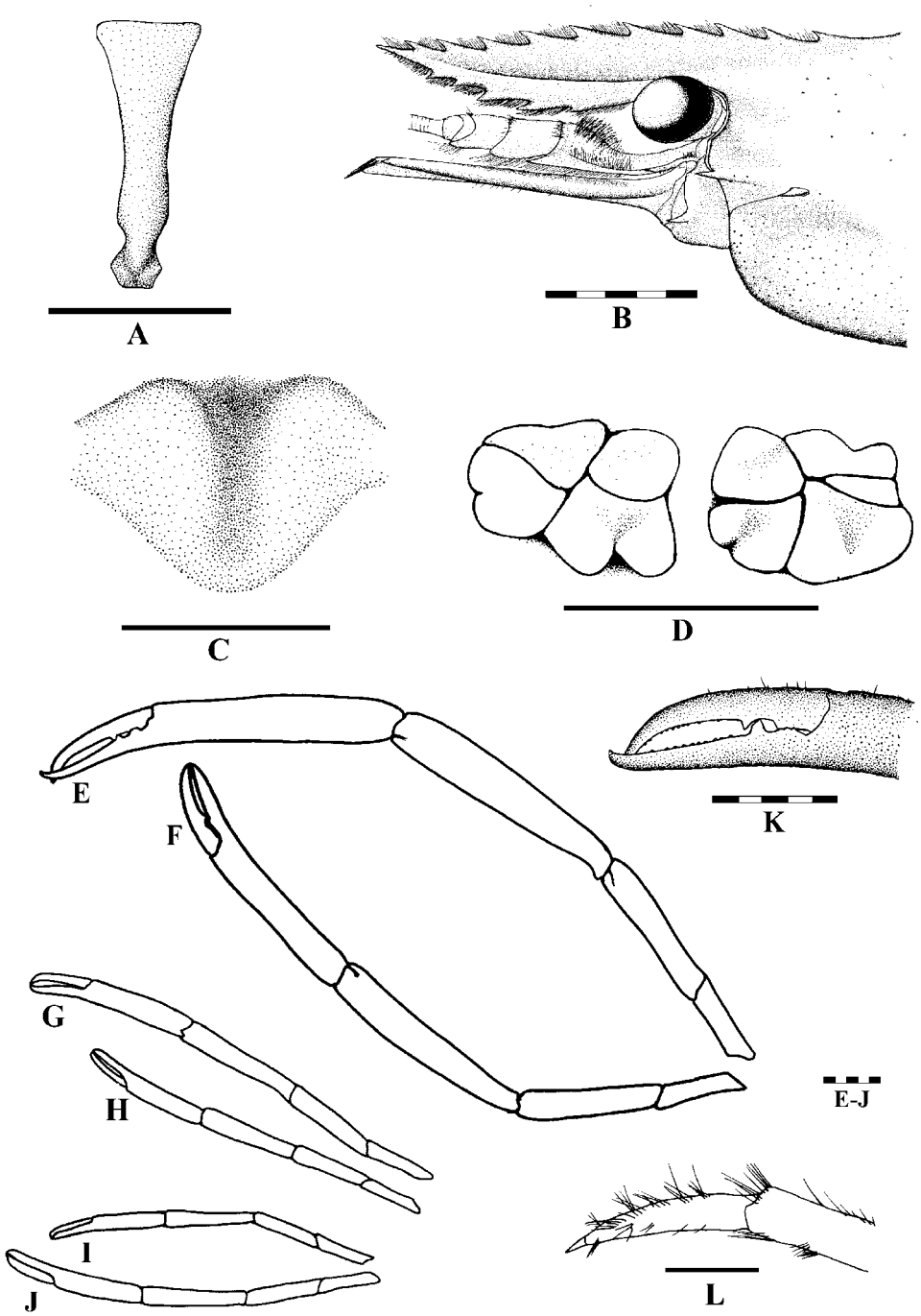

Figure 14. *Macrobrachium bullatum* Fincham, 1989. (A) NTM Cr007327, male 15.6 mm CL, ventral view of inter-uropodal sclerite, (B) anterior cephalothorax of same, (C) epistome of same, (D) QM W16544, male 12.3 mm CL, crowns of left and right mandibular molar processes (setae omitted), (E) NTM Cr005852, male 15.5 mm CL, fully developed right second cheliped (protective setation omitted), (F) fully developed left second cheliped (protective setation omitted), (G) NTM Cr005852, male 15.6 mm, undeveloped right second cheliped (protective setation omitted), (H) undeveloped left second cheliped (protective setation omitted), (I) NTM Cr007412, ovig. female 12.1 mm CL, right second cheliped (protective setation omitted), (J) left second cheliped (protective setation omitted), NTM Cr005852, male 15.5 mm, (K) mesial view of fingers and distal manus of fully developed right cheliped, (L), dactylus and distal propodus of right third pereiopod. Solid scale bars and divisions on divided scale bars 1 mm.

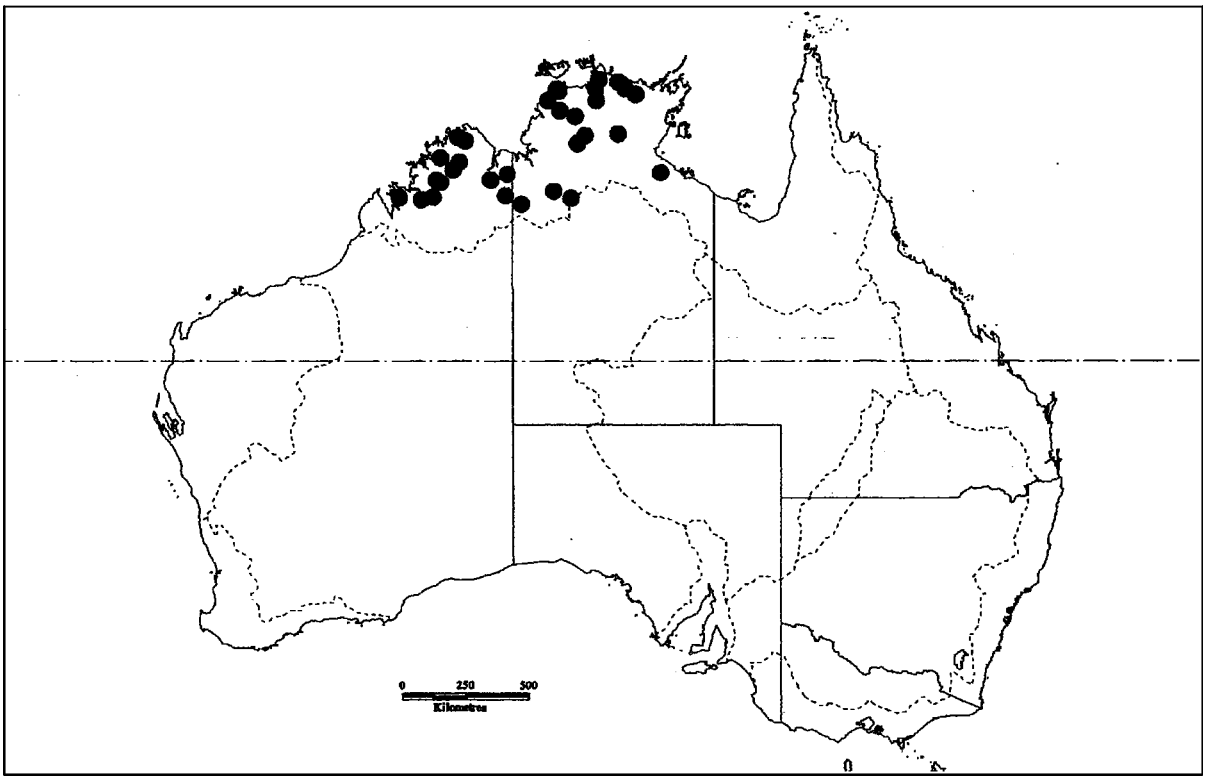

Figure 15. Distribution of *Macrobrachium bullatum* (Fincham, 1989).

Other material

Northern Drainage Region. Lennard R Basin: QM W12638, Barker R., 0.5 km south of Mt Hart Stn; QM W12626, Stewart R., Kimbolton Stn Rd crossing; *Isdell R Basin*: WAM C21737, Beverley Springs Stn, c. 1 km southeast of hmstd; QM W12616, Maudie Ck, Calder R-Mt Elizabeth Stn track; QM W12632, Pearson R., Calder R-Mt Elizabeth Stn track; *King Edward R Basin*: WAM C21459, Carson R. tributary near Doongan Stn at Carson escarpment; QM W12631, Mitchell R., Mitchell R. mining camp; WAM C21736, Mitchell Plateau; QM W12610, Monger Ck, 10 km west of Kalumburu settlement at track crossing; *Drysdale R Basin*: QM W12620, Drysdale R., trucking yards on Kalumburu Rd; QM W12633, Drysdale R., Sandz Crossing; *Pentecost R Basin*: QM W12619, Pentacost R., El Questro Stn; *Ord R Basin*: WAM C11495, Ord R., Lissadell; NTM Cr002658, Lake Argyle; AM P42540, Ord R., Ivahoe crossing, Kununurra; WAM C11520, Behn R., junction with Ord R.; NTM Cr002657, Negri R. crossing; NTM Cr002661, Nicholson R; *Victoria R Basin*: NTM Cr004853, Bullita outstation; NTM Cr005398, Roderick Ck; QM W12615, Lonely Spring Ck, 24 km SW of Top Springs, Buchanan Hwy; NTM Cr005397, East Baines R; *Daly R Basin*: NTM Cr002659, Crocodile Ck, Dorisvale; NTM Cr007294, Daly R., Claravale; NTM Cr005852, Coppermine Billabong; NTM Cr007297, Edith R., above Edith R. falls; *Finniss R Basin*: NTM Cr007328, Cascade Ck, south of Finniss R.; NTM Cr002533, Wangi Falls; NTM Cr002620, Finnis R.; NTM Cr005237, Darwin R. dam; QM W16544, Holmes Jungle near Darwin; QM W16547, Howard Springs area, billabong c. 100 m from creek; *Bathurst and Melville Islands Basin*: QM W24578, Takamprimili Ck upstream of Buffalo Catchers Camp, Melville I; *Adelaide R Basin*: NTM Cr007292, Adelaide R., Beatrice Hill culvert; NTM Cr007299, Humpty Doo area; *Mary R Basin*: NTM Cr007285, Mary R. tributary near Goodparla Stn; NTM Cr002987, McKinley R; *South Alligator R Basin*: NTM Cr002102, Barra-

mundie Ck, Arnhem Land; NTM Cr003086, Barramundie Ck; NTM Cr007307, South Alligator R., Gimbat Stn; NTM Cr007287, South Alligator R., Coronation Hill; NTM Cr005474, Graveside Gorge, Kakadu N.P.; NTM Cr007329, Dook Ck; NTM Cr007393, Jim Jim Ck, Kakadu N.P.; NTM Cr007310, Deaf Adder Ck; *East Alligator R Basin*: NTM Cr007327, Nourlangie Ck, southeast corner of Woolwonga; NTM Cr003092, Tin Camp Ck; *Goomadeer R Basin*: NTM Cr007289, Goomadeer R., crossing on Maningrida-Oenpelli Rd; NTM Cr007291, Goomadeer R. crossing; *Liverpool R Basin*: NTM Cr007296, Nungbalgarri Ck; NTM Cr007302, Nei-Igmut Ck, Arnhem Land; NTM Cr006807, Mann R. crossing, Arnhem Land; NTM Cr007308, Mann R. crossing, Manmoyi camp; NTM Cr007306, Liverpool R; *Blyth R Basin*: NTM Cr007298, Cadell R., road crossing; NTM Cr007305, Blyth R. tributary, Arnhem Land; *Buckingham R Basin*: NTM Cr002155, Giddy R.; *Walker R Basin*: NTM Cr007412, Nathan R; *Roper R Basin*: QM W15023, Flying Fox Ck, Mountain Valley; *Limmen Bight R Basin*: NTM Cr007369, Road crossing south of Nathan River Stn hmstd; *Rosie R Basin*: QM W8609, Lorella Springs, Rosie Ck.

Diagnosis

Rostrum. Short to medium length in fully developed males, developmental range 0.55–0.85 CL; moderately deep (maximum depth slightly more than dorsoventral diameter of eye); dorsal carina convex, dentate along entire length, teeth subequally spaced, 7–10 teeth, 1–2 completely postorbital, all teeth immoveable in fully developed males; ventral carina dentate, (1-) 3–5 teeth, first tooth located in proximal half or at about mid-length.

General cephalon. Ocular cornea large, well-pigmented, accessory pigment spot present. Inferior orbit moderately produced, angular, antennular margin slightly concave or straight. Bec ocellaire strongly developed. Scaphocerite stout, length less than 3 times maximum breadth, lamina distinctly tapering from broadest point to anterior margin, anterior margin produced forward at inner angle. Epistome completely divided into two lobes, lobes produced anteroventrally to blunt apex.

Mouthparts. Third maxilliped terminal segment clearly shorter than penultimate segment; exopod about equal in length to ischiomerus. Mandibular molar process crowns as figured (Fig. 14D).

Second chelipeds (fully developed male). Larger and more developed than female P2; isomorphic in setation and shape, distinctly unequal in length, minor cheliped failing to reach distal end of manus of major cheliped; long, merus of minor cheliped reaching distal end of scaphocerite; bearing protective and simple setae; all segments with abundant well spaced erect mamilliform protective setae, least abundant on lateral surfaces of fingers; simple setae sparsely distributed except for few tufts on fingers; fingers with well developed gape, armed with row of bulliform protective setae submedially along mesial cutting edges; pollex more or less straight, uncinate at tip, not noticeably broadened basally, about equal in breadth to basal dactylus, proximal cutting edge with dentate ridge followed by distinct gap then large tooth, distally entire; dactylus strongly arched, uncinate at tip, proximal cutting edge bearing two large teeth, the first opposing dentate ridge on pollex, the second slightly advanced of large tooth on pollex, distally entire; manus subcylindrical (inflated in holotype male), slightly narrowed distally, maximum breadth clearly greater than maximum merus breadth, much longer than dactylus; carpus much shorter than chela, tapered, often inflated subdistally; merus much shorter than carpus; ischium with well-developed broad median groove on superior face and narrower median groove on inferior face, slightly narrowed at mid-length.

Third pereiopods (fully developed male). Short, reaching distal end of scaphocerite by dactylus at most; lacking protective setae; dactylus elongated, length over four times basal breadth, ventral carina well developed; unguis poorly developed, less than one-fifth length of remainder of dactylus.

Thoracic sternum. T4 with well-developed median process, postcoxal flanges poorly developed, situated posterior to and distinct from median process. Fully developed male T8 with anterolateral lobes widely separated posteromedially, without median process posteriorly (low rounded process present in young males).

Abdomen. Inter-uropodal sclerite without pre-anal carina. Distolateral process on uropodal exopod with accessory spiniform seta mesially.

Body setation (fully developed male). Small mamilliform protective setae present on carapace and abdomen, abundant over most of carapace except posterolateral areas, on abdomen most abundant on tergites 5–6, uropods and telson, more scattered on lower pleura.

Colour

Antennal flagella translucent yellow brown to olive grey. Scaphocerites similar but with olive to blue grey specks distally. Rostrum translucent, lateral carina with olive brown specks. Ocular peduncles with olive brown blotches. Body yellow brown specked with olive brown, lateral carapace with few large irregular olive brown blotches supplemented with numerous smaller blotches, posterodorsal carapace with pair of submedian olive brown blotches, lower pleura of abdomen with small blotches, condyles olive brown, tergite 6 with mid-dorsal olive brown blotch, tailfan translucent yellow-brown specked with light olive brown, dorsal and posterior spiniform setae and posterior margin of telson dark olive brown, uropods tinged with olive brown distally, distolateral process of exopod dark olive brown.

P2 base colour yellow brown to almost white, striped with irregular dark olive brown longitudinal bands running the length of the chelipeds, bands generally located laterally and mesially with a few blotches superiorly and a faint longitudinal band on the superior manus, lighter non-banded areas of superior manus overlaid with a rusty brown reticulated pattern, fingertips light, generally white but varying to orange or green, proximal fingers also with small areas of light base colour overlaid with reticulated pattern similar to on superior manus.

Ambulatory legs translucent, lightly tinged with yellow, ornamented with irregular olive brown blotches, joints of segments lightly tinged with yellow brown, dactyli yellow brown to white.

Life cycle

Restricted to fresh waters, eggs moderately large and few, 28–141 per brood, maximum length of developed ova 1.4 mm. Larval development unstudied but egg size indicative of abbreviated type.

Size

Small species. Maximum size of developed male 20 mm CL, 72 mm TL. Maximum size of female 14 mm CL, 50 mm TL, minimum size of ovigerous female, 7 mm CL.

Habitat ecology

Occurs in a wide range of fresh water habitats including spring-fed, permanently flowing creeks, rivers and plateau streams (to c. 200 m elevation), floodplain billabongs and lagoons, waterholes on seasonal watercourses, man-made reservoirs and lakes. Also recorded from an offshore continental island (Melville Is). Substrates: fine to coarse particle size, including bedrock. Flow: zero to high flow. Water clarity: low to high, generally high in dry season. Water depth: 0.1–2.0 m. Recorded physico-chemical tolerances: water temperature 22–26 °C (field, $n = 12$), pH 6.3–7.8 (field, $n = 13$), hardness <10–150+ ppm (field, $n = 12$). *Fringing vegetation*: open communities dominated by *Eucalyptus*, *Melaleuca*, and *Pandanus* to closed heaths/scrubs and monsoon forest.

Behaviour

Mostly nocturnal and prefers to shelter during daylight in well shaded areas underneath fallen timber, overhanging banks, boulders, rock ledges, or in deep leaf litter beds. Juveniles also found in macrophyte beds.

Distribution

Northwest Australia: Lennard R. basin, W.A. to the Rosie R. basin, N.T.

Systematic position

This species appears closely related to *M. mammillodactylus* as discussed above under that species. Both taxa possess the distinctive rows

of bulliform protective setae (= tubercles of previous authors) submedially on the cutting edges of the fingers of P2 in developed males, a relatively rare character for the genus. The two species are differentiated above under *M. mammillodactylus*.

Vernacular names

Northwest Australian river prawn.

Remarks

M. bullatum was originally described from Magela Ck, Kakadu N.P., Northern Territory by Fincham (1987), based on the male holotype and a female paratype. Fourty additional specimens were also examined by Fincham from the Alligator Rivers region.

The above diagnosis is based on over 400 specimens, including many fully developed males from a much wider geographic range (Kimberley region, W.A. to the Rosie R. basin in the eastern N.T.).

Although the holotype is a large male it is not fully developed as indicated by the limited protective setation on the carapace (normally well developed), glabrous abdominal segments (with protective setation in fully developed males), weak gape between the fingers of the second chelipeds (strong gape in fully developed males), second chelipeds of equal length (distinctly unequal in length in fully developed males), and the merus of the major cheliped not quite reaching to the end of the scaphocerite (longer in fully developed males with the merus of the minor cheliped reaching to the distal end of the scaphocerite). The manus of the holotype is atypically inflated for the species and is more usually, evenly subcylindrical. The holotype also has only two teeth on the ventral margin of the rostrum whereas three or four teeth are more common for the species.

Palaemon australis Roux, 1933, recorded from the Katherine River, N.T. is most likely this species, rather than *M. australiense* Holthuis, 1950.

This is the common land-locked freshwater species in northwest Australia. It is ubiquitous in all permanent freshwater habitats from lowland billabongs to upper catchment headwaters above major waterfalls.

Macrobrachium rosenbergii (De Man, 1879) (Figs 16–18, 36L, M)

Restricted synonymy

Palaemon Rosenbergii De Man, 1879, p. 167.

Macrobrachium rosenbergii – Holthuis, 1950, pp. 18, 105 (key), 111–119, fig. 25a–h (complete earlier literature). 1980, p. 103. Tombes & Foster, 1979, pp. 179–184, pls 1, 2. Liu et al., 1990, pp. 103 (key), 104, fig. 1. Ng & Choy, 1990, pp. 303 (key), 307, fig. 2F, 4D. Shy & Yu, 1998, p. 43.

Macrobrachium rosenbergi (sic) – Riek, 1951, pp. 360 (key), 361, fig. 12.

Macrobrachium rosembergii (sic) – Maccagno & Cucchiari, 1957, pp. 278 (key), 355–358, fig. 44.

Material examined

Northern Drainage Region. Fitzroy R Basin: QM W12628, Geikie Gorge, 0.5 km upstream from N.P. boundary; WAM C21443, Fitzroy R., Broome-Derby Rd crossing; WAM C21450, Fitzroy R., Langey Crossing; QM W12611, Fitzroy R.; WAM C7185, Langi Ck; WAM C21705, May R. near Derby; WAM C11527, 8 km southeast of Derby; WAM C11548, Derby near jetty; WAM C12096, Yeeda Ck, 6 km downstream of Yeeda hmstd; *Lennard R Basin*: WAM C11534, Mt Hart Stn, creek near hmstd; *Prince Regent R Basin*: WAM C21445, Prince Regent R., WAM C21448, King Cascades, Prince Regent R.; WAM C21708, East Gorge Ck, Prince Regent River N.P.; WAM C21707, Prince Regent R. N.P.; *King Edward R Basin*: WAM C21446, Wyulda Ck and Roe R. junction, Prince Regent River N.P.; WAM C21449, Kalumburu near Mission; WAM C24365, Kalumburu; *Drysdale R Basin*: WAM C21706, Drysdale R.; WAM C21447, Mogurnda Ck and Drysdale R. junction, Drysdale N.P.; QM W12634, King George R., top of Gorge Falls; *Ord R Basin*: WAM C11529, Ord R. near Lake Argyle; WAM C11528, Ord R; WAM C12103, Ord R., below Great Northern Hwy crossing; *Keep R Basin*: NTM Cr012775, Cockatoo Lagoon, Keep R.; *Victoria R Basin*: NTM Cr005395, Gregory Ck; NTM Cr005404, Fig Tree Ck; NTM Cr012776, Victoria R.; *Daly R Basin*: NTM Cr002107, Daly R., Oolloo crossing; NTM Cr005529, Daly R., Claravale; NTM Cr005850,

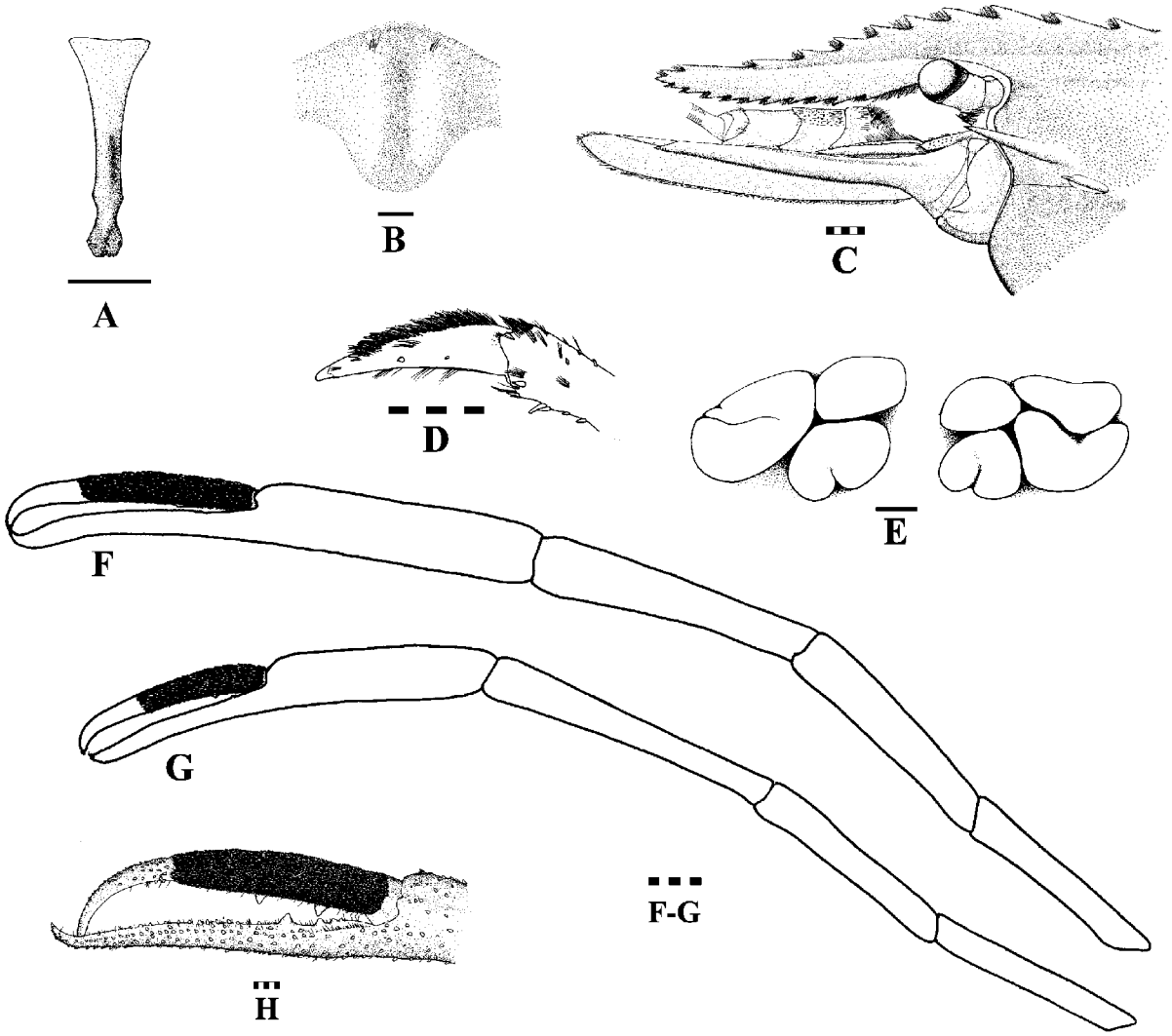

Figure 16. *Macrobrachium rosenbergii* (De Man, 1879). (A) QM W16848, male 27.5 mm CL, ventral view of inter-uropodal sclerite, (B) QM W16621, male 71.9 mm CL, epistome, (C) QM W16487, male 83.3 mm CL, anterior cephalothorax, (D) QM W16487, male 83.3 mm CL, dactylus and distal propodus of right third pereiopod, (E) QM W16621, male 71.9 mm CL, crowns of left and right mandibular molar processes (setae omitted), (F) QM W22028, undeveloped male 45.0 mm CL, right second cheliped (protective setation omitted), (G) female 42.3 mm CL, right second cheliped (protective setation omitted), (H), QM W16487, male 83.3 mm CL, mesial view of fingers and distal manus of fully developed right cheliped. Solid scale bars and divisions on divided scale bars 1 mm.

Coppermine Billabong; NTM Cr012777, Fergusson R; NTM Cr012778, Fish R., 145 km WNW of Katherine; *Finniss R Basin*: NTM Cr001718, Berry Springs; *Adelaide R Basin*: QM W12584, Jasper Ck, c. 27 km WNW of Kidman Springs; NTM Cr006752, Adelaide R., Mt Bundey; *South Alligator R Basin*: NTM Cr004413, South Alligator R., Gimbat Stn; NTM Cr004412, South Alligator R., Coronation Hill; *East Alligator R Basin*: NTM Cr002110, East Alligator R.; NTM Cr002053, Radon Ck, Mt Brockman; NTM Cr007391, Mainoru R., Bulman Rd; NTM Cr012779, Cooper Ck; *Liverpool R Basin*: NTM Cr006809, Liverpool R; NTM Cr006796, Mann R. crossing, Arnhem Land; NTM Cr006797, Mann R., Kubumi Waterhole; *Blyth R Basin*: NTM Cr006792, Blyth R.; *Roper R Basin*: AM P11861, Mataranka; QM W19663, Roper R.; *McArthur R Basin*: SAM

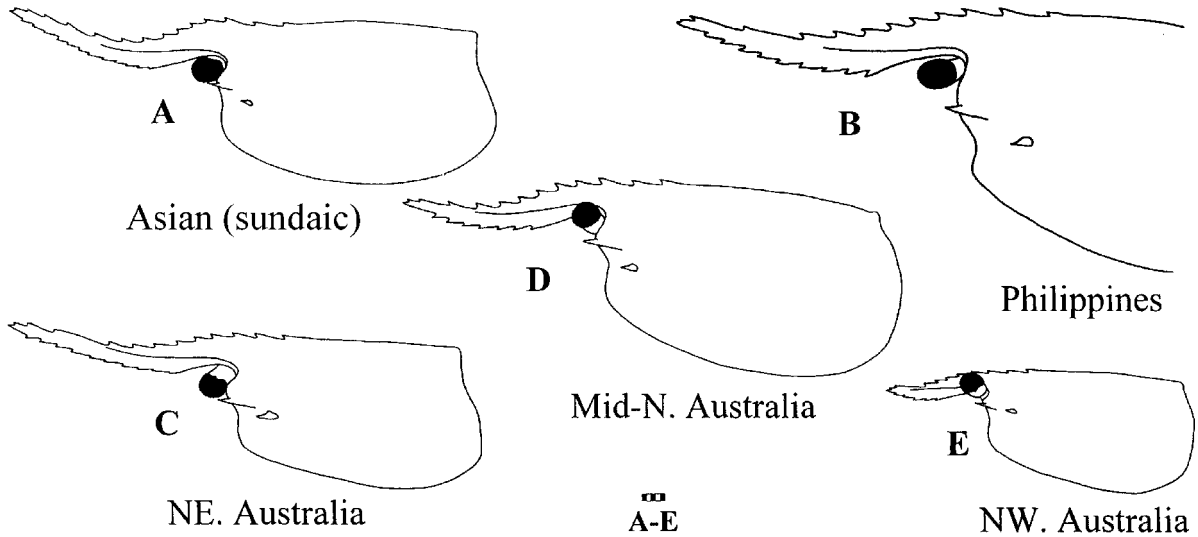

Figure 17. Geographical rostrum variation in mid-grown, sexually-mature males of *Macrobrachium rosenbergii* (De Man, 1879). (A) QM W17187, 58.1 mm CL, Kelian R., Kalimantan, (B) 245–250 mm TL, Philippines (after Cowles, 1914), (C) QM W22028, 45.0 mm CL, McIvor R., northeast Australia, (D) NTM Cr005849, 58.5 mm, Coppermine Billabong, Daly R. catchment, mid-northern Australia, (E) WAM C21445, 43.2 mm, Prince Regent N.P., northwest Australia. Scale bar divisions 1 mm.

TC11159, McArthur R., c. 2 km from Cattle Stn; AM P42538, Ryans Bend; *Nicholson R Basin*: QM W12614, Gregory R., Riversleigh Stn; QM W1163, Gregory R., Burke District; *Leichhardt R Basin*: QM W15163, Leichhardt R., crossing near Nardoo Stn; QM W7999, Leichhardt R. at Leichhardt Falls, Floraville Stn; *Norman R Basin*: QM W15311, Norman R., Normanton; QM W7251, Norman Ck, Normanton Rd; QM W2082, Norman R.; QM W11966, Norman R., upstream limit of Glenore storage; QM W14937, Walker Ck near Normanton; *Gilbert R Basin*: QM W10454, Fossilbrook Ck, Burlington Stn near Mt Surprise; *Mitchell R Basin*: QM W16398, Lynd R.; QM W7892, Mt Molloy; QM W5434, Spear Ck near Mt Molloy; QM W3063, Rifle Ck near Mt Molloy; QM W11967, Mitchell R.; *Holroyd R Basin*: QM W11975, Holroyd R. tributary; QM W16400, Pretender Ck; *Archer R Basin*: QM W16695, Archer R., Peninsula Developmental Rd crossing; QM W11976, Archer R.; QM W12870, Coen R.; *Watson R Basin*: QM W9714, Coconut Ck, north of Camp Beagle, c. 64-77 km north of Aurukun; *Wenlock R Basin*: QM W11964, Wenlock R.; QM W16622, Wenlock R., Peninsula Developmental Rd crossing; QM W16848, Wenlock R., Stones Crossing; QM W8856, Dulhunty R.; QM W16701, Dulhunty R., telegraph line crossing; *Ducie R Basin*: QM W16390, Cockatoo Ck, c. 70 km south of Bamaga.

Eastern Drainage Region. Olive-Pascoe Rivers Basin: QM W22243, Olive R.; *Normanby R Basin:* QM W16623, Normanby R., Orange Plain Waterhole; QM W16397, East Normanby R., c. 40 km SW of Cooktown; QM W3993, Hann R.; QM W16621, Hann R., Peninsula Developmental Rd; QM W11980, Kennedy R., Hann Crossing; *Jeannie R Basin*: QM W22028, McIvor R., Isabella-McIvor Rd crossing.

Diagnosis

Rostrum. Short in fully developed males (Australian populations), developmental range 0.42–1.65 CL; moderately deep in distal half (maximum depth slightly more than dorsoventral diameter of eye), moderately developed basal crest above eye (well developed in Asian forms); dorsal carina generally sinuous, sometimes upturned or convex proximally and straightened distally, dentate along entire length, 8–15 teeth, 2–3 completely postorbital, teeth tending to be more closely spaced proximally above orbit than subdistally, distally with several closely-spaced api-

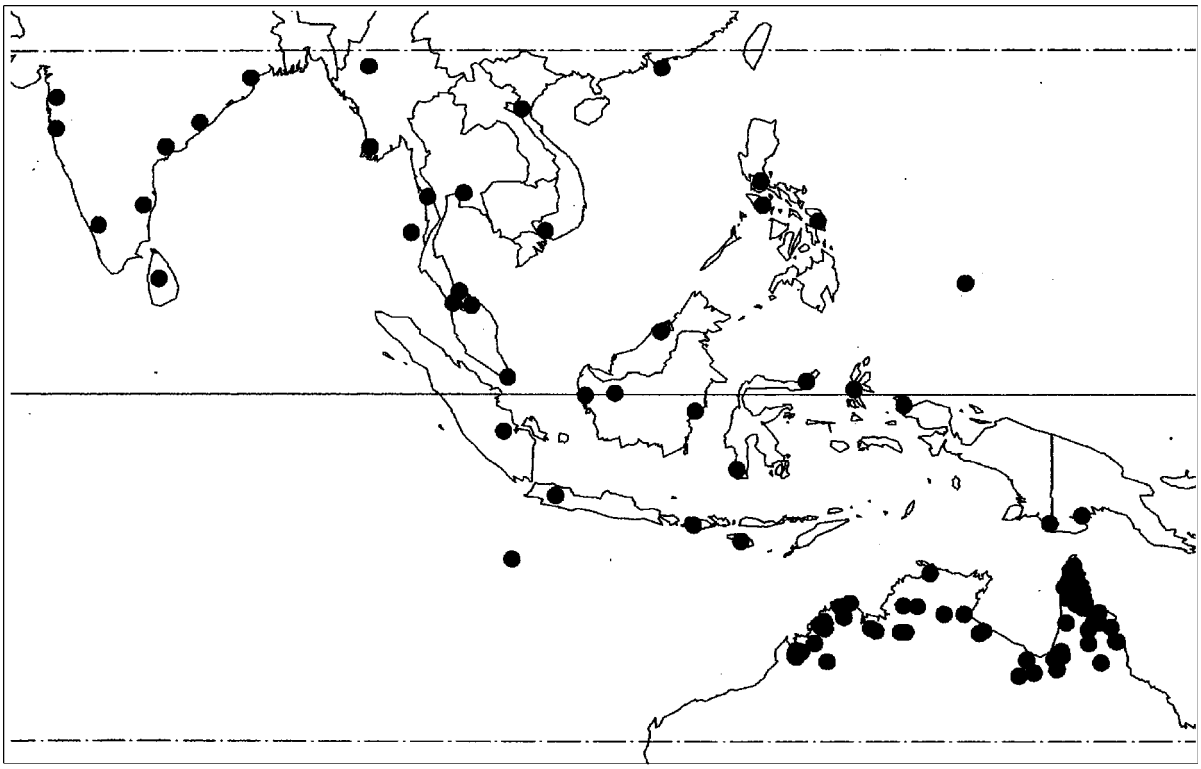

Figure 18. Distribution of *Macrobrachium rosenbergii* (De Man, 1879).

cal teeth, all teeth immoveable in fully developed males; ventral carina dentate, (3-) 5–11 teeth (Australian material; 8–15 Asian forms), first tooth generally located well within proximal half.

General cephalon. Ocular cornea large, well-pigmented, accessory pigment spot present. Inferior orbit moderately produced, variable in shape, generally angular with post-antennular carapace margin concave or straight in developed males, sometimes obtuse, slightly angular above and rounded below in younger specimens. Bec ocellaire strongly developed. Scaphocerite stout, length less than three times maximum breadth, slightly tapered from broadest point to anterior margin, anterior margin strongly produced forward at or near mid-line. Epistome completely divided into two lobes, lobes with low broad longitudinal carinae.

Mouthparts. Third maxilliped terminal segment clearly shorter than penultimate segment; exopod about equal in length to ischiomerus. Mandibular molar process crowns as figured (Fig. 16E).

Second chelipeds (fully developed male). Larger and more developed than female P2; isomorphic (may be subequal in length); long, merus reaching distal end of scaphocerite; with protective, simple and pappose setae; all segments except dactylus and ischium with abundant spinuliform protective setae interspersed with widely-spaced, elevated, spiniform, protective setae, elevated setae most developed and widely spaced on superomesial surfaces, least developed and most closely spaced on inferolateral manus and carpus, ischium with widely spaced, elevated, spiniform protective setae, spinuliform protective setae largely absent; pappose setae forming velvety pubescence on proximal two-thirds to three-quarters of dactylus, absent on pollex; simple setae scattered except for few tufts on distal fingers; pollex elongated, slightly sigmoidal, not noticeably broadened basally, about equal in breadth to basal dactylus, uncinate at tip, proximal cutting edge with ridge of two or three small teeth followed by distinct gap then large tooth, distally entire; dactylus elongated, strongly uncinate at tip, crossing pollex well before tip,

proximal cutting edge with two large teeth, the first opposing ridge of teeth on pollex, the second slightly advanced of large tooth on pollex, distally entire; manus subcylindrical, much longer than dactylus, maximum breadth c. equal to maximum merus breadth; carpus clearly shorter than chela, elongated, tapered; merus clearly shorter than carpus, elongated, tapered, inflated distally; ischium of moderate length, with well developed median groove on both superior and inferior faces, compressed.

Third pereiopods (fully developed male). Short, dactylus reaching distal end of scaphocerite; covered with abundant elevated, spiniform protective setae; dactylus elongated, length four or more times basal breadth; unguis poorly developed, less than one fifth length of remainder of dactylus.

Thoracic sternum. T4 with well-developed median process, postcoxal flanges situated posterior to and distinct from median process. Fully developed male with anterolateral lobes contiguous posteromedially, without median process posteriorly (rounded process present in young males).

Abdomen. Inter-uropodal sclerite with low, rounded, pre-anal carina. Distolateral process on uropodal exopod with accessory spiniform seta mesially.

Body setation (fully developed male). Protective setation well developed on carapace and abdomen, numerous spinuliform protective setae over most of carapace except hepatic region, abdomen with spinuliform protective setae on pleura, uropods and telson.

Colour

Live colouration of Australian specimens differ notably from that described for the 'western' or 'Asian' race but are closer to the colour described by Cowles (1914) for the Philippines form. Young specimens in Australian populations develop a chromatophore pattern of longitudinal stripes on the carapace and mottling on abdomen which then disappears in adults, similar to that described by Hiramatsu et al. (1985) for Asian stock. In young specimens the flagella are cream coloured except for the inner antennular flagella which are dark olive grey. The scaphocerites are cream tinged with orange brown. The peduncles are cream with orange brown specks. The rostrum is translucent cream with orange brown specks, particularly along the lateral carina. The carapace is cream with longitudinal blue grey stripes and the abdomen olive grey mottled with indistinct bluish grey blotches. The pleural condyles are orange brown.

The first chelipeds and ambulatory legs are cream with orange brown specks, the joints are orange brown. The second chelipeds are also cream with orange brown specks on the ischium, the merus is a drab grey becoming violet brown or bluish brown distally, the carpus is a drab grey tinged with violet brown or bluish brown becoming violet brown distally, the manus is violet to bluish grey marked with cream at the articulation with the carpus and mauve distally at the base of the pollex and dactylus, the fingers are deep blue except for red at the articulation of the dactylus.

Adult males and females are uniformly olive brown on the carapace and abdomen with distinctive dark pigment spots underneath the base of rostrum and on the hepatic regions on each side of carapace.

The second pereiopods change from brown in undeveloped males to bright violet in developing males through to the dark violet brown or almost black in fully developed males. This contrasts with the well-defined deep blue colour of the chelipeds of developed males and the orange colour of subordinate males described for Malaysian stock by Kuris et al. (1987). The abdomen is also said to have blue crossbands (Khandker and Patra, 1971) in mainland Asian populations.

Life cycle

Catadromous, ovigerous females migrating to brackish water to release larvae (Rao, 1967; George, 1969); eggs small to moderately large, numerous, up to 150 000 per brood (Ling & Merican, 1961), maximum length of developed ova 0.7 (Asian form), 0.9 mm (populations from the Darwin area, mid-northern Australia) to 1.3 mm (northwest Australian form, Lennard River basin); larval development extended (Asian form), 11 planktonic stages, 16–36 days, optimum tempera-

ture range 26–31 °C, optimum salinity 12 ppt (New & Singholka, 1985).

Size

Large species. Maximum size of developed male 84 mm CL (this study), 260 TL (this study) – 320 mm TL (Holthuis, 1980). Maximum size of female 250 mm TL (Holthuis, 1980).

Habitat ecology

This species shows a broad altitudinal distribution from lower estuaries to upland fresh waters (to 430 m elevation), including floodplain billabongs, waterholes and large pools on seasonally flowing rivers, permanently flowing, spring-fed rivers and creeks, and large tidal rivers. Substrates: fine to coarse, including bedrock. Flow: zero to high flow. Water clarity: low to high. Water depth: 0.1–3.7 m. Recorded physico-chemical tolerances: hardness <10–80 ppm (field, $n = 4$), water temperature 14–35 °C (New & Singholka, 1985), DO_2 1.5–8.6 ppm (field, $n = 3$), pH 5.0–8.0 (field, $n = 22$). Fringing vegetation: open communities dominated by *Eucalyptus*, *Melaleuca*, *Pandanus*, to closed monsoon forest and mangroves.

Behaviour

Nocturnal, prefers to shelter during daylight in well shaded areas underneath fallen timber, overhanging banks, boulders, rock ledges. Agonistic behaviour, the formation of dominance hierarchies and infraspecific competition has been studied by Peebles (1979, 1980), Karplus and Harpaz (1990) and Barki et al. (1991a, b); reproductive behaviour by Rao (1965) and Ra'anan & Sagi (1985); feeding behaviour by Moller (1978) and Harpaz et al. (1987) and circadian rhythmicity by Nakamura (1975).

Distribution

Wide-ranging Indo-West Pacific: India to southern China, the Philippines, Indonesia, New Guinea and Palau. *Australian distribution:* Fitzroy R. basin, W.A. to the Jeannie R. basin, Qld.

Systematic position

This species appears closely allied to *M. gangeticum* Bate, 1868, and *M. malcolmsonii* (H. Milne Edwards, 1844). The taxonomic relationship of *M. rosenbergii* to the Indo-Burmese nominal species, *M. birmanicum* (Schenkel, 1902) and *M. villosimanus* (Tiwari, 1949) is unclear and requires further study.

Among Australian species, *M. rosenbergii* is a highly distinctive taxon, easily distinguished by the shape of the anterior scaphocerite, very large body size, and the velvety pappose setation on the proximal two-thirds of the dactylus of developed male P2.

Vernacular names

Giant river prawn (FAO); Cherabin (Kimberley, Australia); Giant freshwater prawn/shrimp (U.S.A.); Golda chingri, Mocha chingri (Calcutta, India; Bangladesh); Bharo chingri (or Bara chingri), Chooan chingri, Mota chingri, Shala chingri (Bangladesh); Udang satang, Udang duri (Java, Indonesia); Udang galah (Malaya, Borneo, Indonesia), Koong yai (Thailand) (Holthuis, 1980).

Remarks

Macrobrachium rosenbergii (De Man) is the world's largest and most studied river prawn, due largely to its commercial importance in the aquaculture industry. Aquaculture of the species was pioneered by Ling (1969) using Malaysian stock in Hawaii, followed by a mass culturing technique developed by Fujimura and Okamoto (1972). New & Singholka (1985) published a culture manual for the species. Other important references on the culture of this species include Goodwin & Hanson (1975), Hanson & Goodwin (1977) and New (1982). Despite this high level of interest in aquaculture over the last three decades, much more work is still required to adequately document geographical variation in the species.

De Man's original description was based on a single adult female from Western New Guinea. Cowles (1914) provided an extensive description of the Philippines form under the name, *Palaemon carcinus* Linnaeus, by which it was widely known

in the early literature. Holthuis (1950) clarified the differences between *M. carcinus* (Linnaeus) from West Atlantic drainages and the Indo-West Pacific species, *M. rosenbergii* (De Man). The first Australian record was by Roux (1933) from the Katherine River, N.T.

M. rosenbergii shows a high degree of infraspecific geographical variation in the shape and length of the rostrum, second cheliped shape, body and second cheliped colour and life history. Johnson (1973) erected a new subspecies *M. rosenbergii schenkeli* for western Asiatic populations (type locality Tavoy, Burma) and limited the nominotypical subspecies to New Guinea, Australia and possibly Wallacea. Holthuis (1995) made no mention of Johnson's subspecies and stated 'So far no suggestions have been made for the name of the western subspecies'. He proposed the usage of the name *Palaemon d'Acqueti* Sunier, 1925, for the western subspecies and erected a lectotype for Sunier's taxon. The type locality was given as 'Batavia' (=Jakarta, Java, Indonesia). Unfortunately, significant geographic variation has been noted between western Asian populations (Wong & McAndrew, 1990). This makes it less than clear that Johnson's and Sunier's subspecies should be treated as synonyms.

Lindenfelser (1984) provided further support for eastern and western subspecies and gave the boundary between the two as Wallace's line. The Philippines form, despite its close proximity to mainland Asia, was placed in the eastern nominotypical subspecies. Unfortunately geographic variation within Australian populations was no discussed – only two Australian localities were sampled, both in northwest Australia.

An examination of over 280 specimens from localities across northern Australia (Fitzroy River, W.A. to the McIvor River, NE.Qld) during this study revealed a high degree of infraspecific variation. Northwest Australian populations from the Fitzroy River, W.A. to the Keep River, N.T. have a very short rostrum and low rostral formula (8-12/5-8) as compared to northeast Australian populations from the Roper River, N.T. to Normanby R., Qld (11-14/8-10). Whilst the rostral formula for the northwestern Australian race is largely outside the range diagnostic for the species (Holthuis, 1950; Chace & Bruce, 1993) and closer to *M. malcolmsonii*, the form of the chelipeds is still close to *M. rosenbergii rosenbergii*. The size of the ova recorded for an ovigerous female from the Lennard River basin in the western Kimberley is much larger (1.3 mm maximum length) than previously described for the species (0.7 mm maximum length) by New & Singholka (1985) and (Cowles, 1914). The larval cycle in the northwestern Australian race is also said to be more abbreviated than typical for the species (R. Emiliani, pers. com.). The northeastern race agrees with the rostral formula of De Man's type female from New Guinea and that provided for the Philippines form (Cowles, 1914). Between the Keep River and the Roper River, N.T., there appears to be one or more intermediate forms. The rostral formal for populations from this zone is 10-13(-14)/(5-)6-8(-11). Within this zone, populations from the Darwin area have moderately large ova (0.9 mm maximum length) which are significantly larger than Asian populations but much smaller than the northwestern Australian race. Unfortunately, I have not had the opportunity to examine ova from northeastern Australian populations.

Clearly, although *M. rosenbergii* is undergoing morphological divergence, delimiting subspecies is not a straightforward task. In rostrum length and dentition there appears to be a step cline, with the western Asian form at one end and the northwest Australian form at the other end. Somewhere in the middle of the cline fall the New Guinea, Philippines and northeast Australian forms. Broad areas of intergradation may occur in mid-northern Australia and possibly in the region of Wallace's line as indicated by Johnson (1973): 'The single specimen from Bali in the British Museum collections seems to be somewhat intermediate between the two (subspecies)'.

Johnson (1973) reports that both young and adults have been taken in fully marine coastal waters. In this study an adult female has been examined from Derby, W.A. (WAM C11548), a marine locality. The species has also been recorded from two relatively isolated island localities, Palau in the northwest Pacific and Christmas Island in the northeast Indian Ocean, suggesting marine dispersal capability. This contradicts Lindenfelser (1984) suggestion that 'neither larvae nor adults can tolerate seawater and populations are fairly well isolated (S. Malecha, pers. comm.)'. Inshore marine

dispersal of the species by both young and adults appears likely. Discontinuities in clinal variation could be expected to occur between land masses separated by deep or wide oceanic areas or in arid regions where river systems are widely separated.

Considering the high level of interest in the aquaculture of the species it would be desirable to have formal subspecific names for all geographical variants showing significant variation in life history and morphology. However, this will require a comprehensive study of populations throughout the broad range of the species.

Macrobrachium australiense Holthuis, 1950 (Figs 19–22, 36D)

Palaemon sp.? – Ortmann, 1891, p. 708.

Palaemon australis – Ortmann, 1891, p. 709 (not Guérin-Méneville, 1838). 1894, p. 17. McNeill, 1926, p. 325, fig. Hale, 1927a, p. 60, fig. 56; 1927b, p. 309.

Palaemon (Parapalaemon) australis – McNeill, 1929, p. 144, pl. 35.

Palaemon ornatus – Baker, 1914, p. 447 (not Olivier, 1811).

Macrobrachium australiense Holthuis, 1950, pp. 13, 108 (key), 174–176 (in part). Short, 1995, p. 48; 2000, p. 63. Cook et al., 2002, pp. 2098–2112, fig. 1–4.

Macrobrachium adscitum adscitum Riek, 1951, pp. 360 (key), 363, fig. 3. Fincham, 1987, p. 353 (key).

Macrobrachium adscitum subsp. Riek, 1951, p. 363.

Macrobrachium atactum atactum Riek, 1951, pp. 360 (key), 364, fig. 5. Fincham, 1987, p. 353 (key).

Macrobrachium atactum ischnomorphum Riek, 1951, pp. 360 (key), 364, fig. 6. Fincham, 1987, p. 353 (key).

Macrobrachium atactum sobrinum Riek, 1951, pp. 360 (key), 364–365, fig. 7. Fincham, 1987, p. 353 (key).

Macrobrachium australiense australiense – Riek, 1951, pp. 360 (key), 365, fig. 10. Fielder, 1970, pp. 60–74, figs 1–5. Fincham, 1987, p. 353 (key).

Macrobrachium australiense crassum Riek, 1951, pp. 360 (key), 366, fig. 11. Fincham, 1987, p. 353 (key).

Macrobrachium australiense cristatum Riek, 1951, pp. 360 (key), 366, fig. 9. Fincham, 1987, p. 353 (key).

Macrobrachium australiense eupharum Riek, 1951, pp. 360 (key), 365, fig. 8. Fincham, 1987, p. 353 (key).

not *Palaemon australis* – Roux, 1933, p. 344 (? = *M. bullatum* Fincham, 1987).

Material examined

Holotype of *M. adscitum adscitum* Riek, 1951. *Murray-Darling Drainage Region*. AM P3095, 1 male, CL 19.3 mm, Accommodation Ck near Ballandean, W. Garwith, before 1912.

Holotype of *M. atactum atactum* Riek, 1951. *Eastern Drainage Region*. *Mary R Basin*: AM P12007, 1 male, CL 22.0 mm, Mary R., Conondale, E.F. Riek, 25/4/1943.

Holotype of *M. atactum ischnomorphum* Riek, 1951. *Eastern Drainage Region*. *Maroochy R Basin*: AM P11995, 1 male, CL 20.6 mm, Elimbah Ck (= Six Mile Ck?), Elimbah, E.F. Riek, 33/4/1943.

Holotype of *M. atactum sobrinum* Riek, 1951. *Lake Eyre Drainage Region*. AM P11998, 1 male, CL 19.9 mm, Muttaburra, from river, E.F. Riek, 27/5/1945.

Holotype of *M. australiense crassum* Riek, 1951. *Eastern Drainage Region*. *Barron R Basin*: AM P12010, 1 male, CL 24.4 mm, Cairns, Wassell, 30/1/1946.

Holotype of *M. australiense cristatum* Riek, 1951. *Murray-Darling Drainage Region*. AM P12004, 1 male, CL 17.3 mm, Pallal, Horton R. near Bingara, A.R. McCulloch.

Holotype of *M. australiense eupharum* Riek, 1951. *Eastern Drainage Region*. *Burdekin R Basin*: AM P12001, 1 male, CL 15.6 mm, Burdekin R., Macrossan, E.F. Riek, October 1943.

Other Material. *Northern Drainage Region*. *Fitzroy R Basin*: WAM C21441, Minnie R., Broome-Derby Rd crossing; WAM C21442, Fitzroy R., Broome-Derby Rd crossing; *Pentecost R Basin*: AM P54999, Pentecost R., El Questro Stn; *Ord R Basin*: WAM C11520, Behn R., junction with Ord R.; WAM C11486, Argyle Downs Stn, 11 km west of hmstd; WAM C11518, Stackyard Pool, Ord R. area; WAM C11482, Old Lissadell crossing, 3 km north of; *Victoria R Basin*: Cr002656,

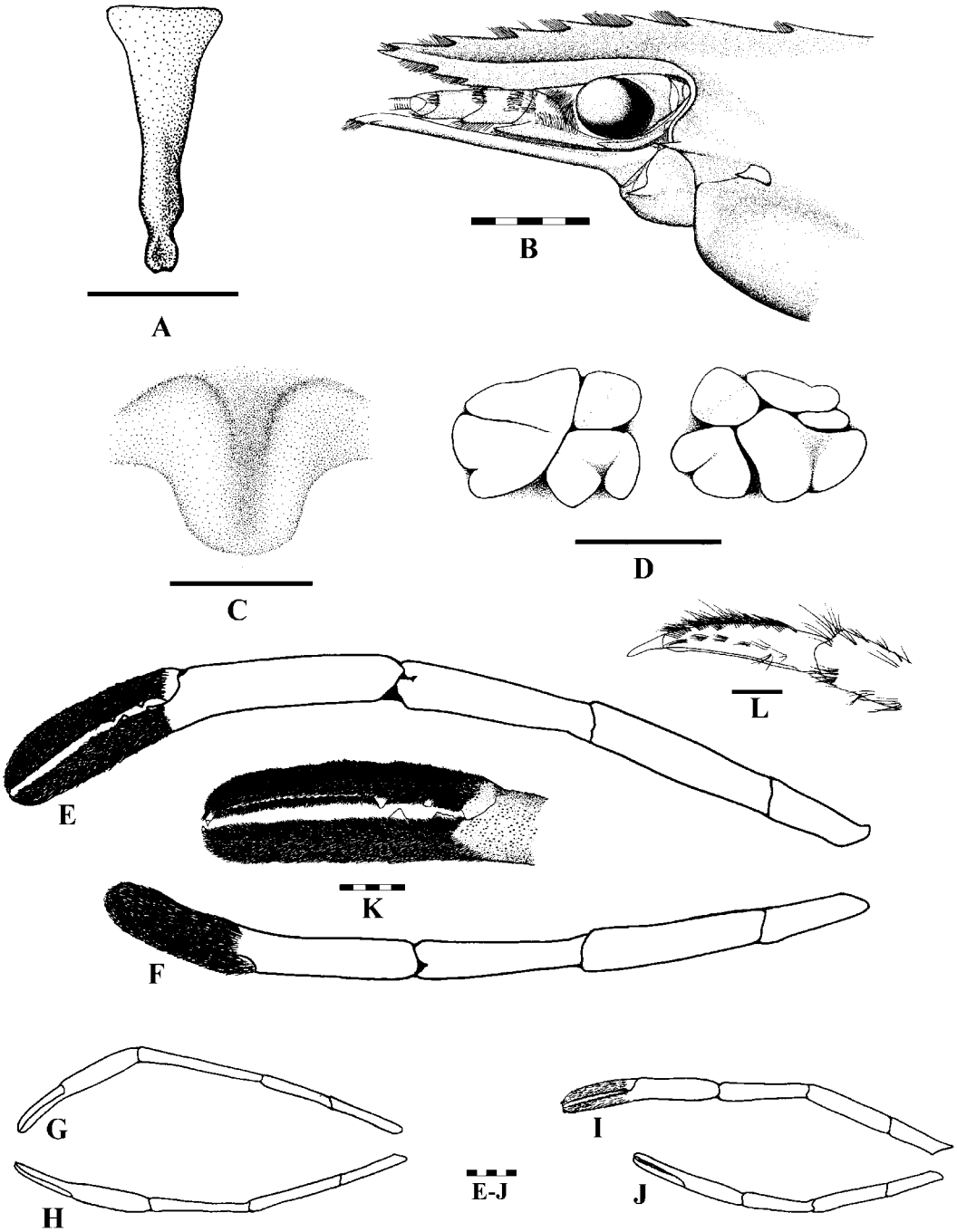

Figure 19. *Macrobrachium australiense* Holthuis, 1950. (A) QM W17248, male 18.6 mm CL, ventral view of inter-uropodal sclerite, (B) QM W15504, male 22.1 mm CL, anterior cephalothorax, (C) QM W16525, male 17.6 mm CL, epistome, (D) crowns of left and right mandibular molar processes (setae omitted) of same, (E) QM W16494, male 26.9 mm CL, fully developed major second cheliped (protective setation omitted), (F) fully developed minor second cheliped (protective setation omitted). QM W19652, ovigerous female 15.6 mm CL, (G) right second cheliped (carpus abnormally long, protective setation omitted), (H) left second cheliped (protective setation omitted), (I) QM W15504, male 14.7 mm CL, undeveloped major second cheliped, (J) undeveloped minor second cheliped, (K) QM W16494, male 26.9 mm CL, mesial view of fingers and distal manus of fully developed major cheliped, (L) dactylus and distal propodus of fully developed right third pereiopod. Solid scale bars and division on divided scale bars 1 mm.

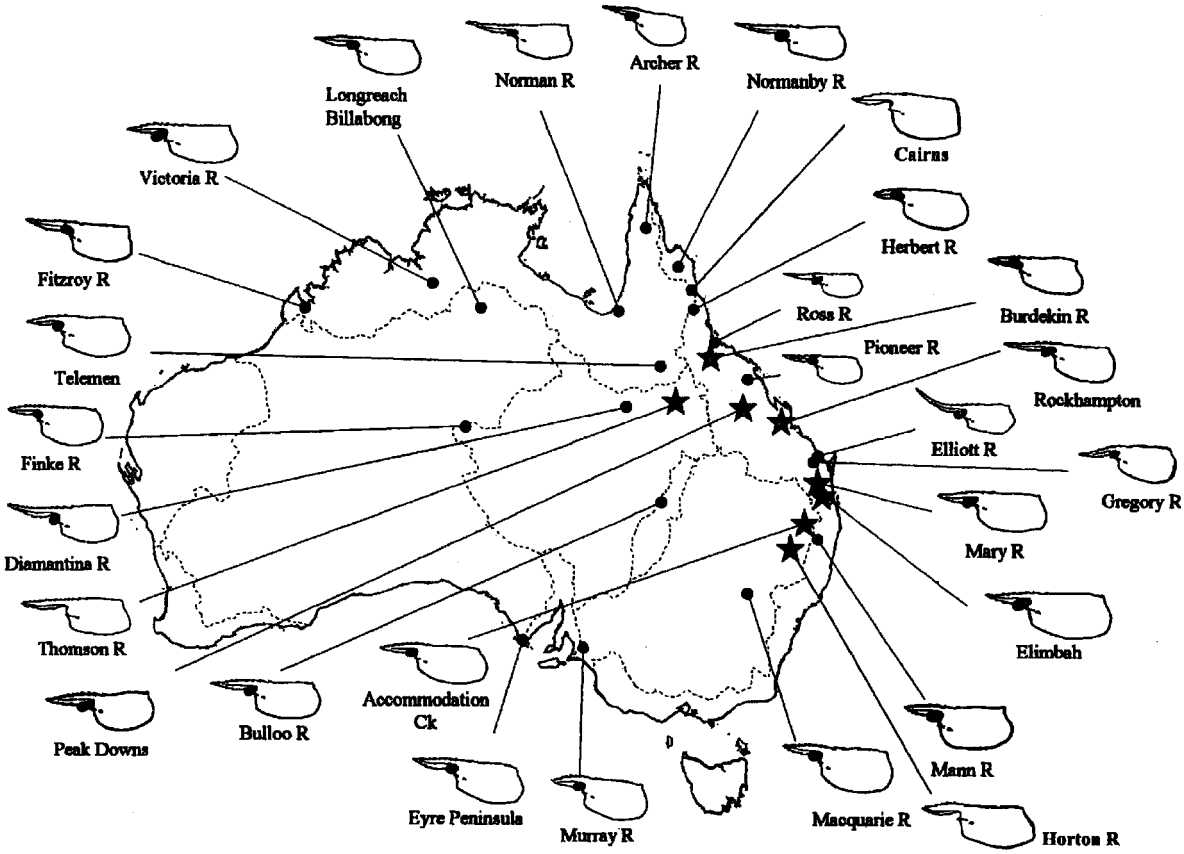

Figure 20. Geographical rostrum variation in *Macrobrachium australiense* Holthuis, 1950. Type localities of synonymised taxa are indicated by star symbols. Specimens figured are not necessarily typical of each population but instead illustrate the degree of geographic variation possible between localities. Figures from the Thomson R., Horton R. and Cairns are after Riek (1951).

Wattie Ck, Wave Hill; *Calvert R Basin*: AM P42524, Calvert R., road crossing; *Nicholson R Basin*: QM W7297, Gregory R., crossing between Lawn Hill and Riversleigh Stn; QM W20656, Gregory R. at Gregory Downs Stn crossing; QM W20649, Lawn Hill Ck, Lawn Hill N.P., just above upper Gorge; QM W20652, Mussellbrook Ck near Mussellbrook Mining Camp, Lawn Hill N.P.; QM W20653, QM W11966, Norman R., upstream limit of Glenore storage; *Leichhardt R Basin*: QM W8019, Leichhardt R.; QM W19655, Leichhardt Falls, Leichhardt R., Floraville Stn; SAM C5849, Creek 86 km east of Leichhardt Falls on Normanton-Burketown Rd; SAM C5850, Lake Waggaboonya near Gunpowder, NW of Mt Isa; *Flinders R Basin*: QM W570, Telemen; *Gilbert R Basin*: QM W11969, Einasleigh R., Carpentaria Downs Stn; QM W9283, Fossilbrook Ck; QM W10455, Fossilbrook Ck, Burlington Stn near Mt Surprise; QM W14935, Mt Surprise area; *Mitchell R Basin*: QM W15503, Walsh R., Mareeba-Dimbulah Rd bridge; QM W16624, Rifle Ck near Mt Molloy; QM W5417, Crowleys Ck, 5 km east of Mt Molloy; QM W16627, Mary Ck, Mt Carbine-Mt Molloy Rd; QM W19267, West Spencer Ck; QM W16626, Palmer R., Palmer R. roadhouse; QM W16092, Mitchell R.; QM W11974, Mitchell R., Highway Stn; *Archer R Basin*: QM W16696, Archer R., Peninsula Developmental Rd crossing; QM W16693, Lankelly Ck, Coen; *Wenlock R Basin*: QM W19657, Wenlock R.

Eastern Drainage Region. Olive-Pascoe Rivers Basin: QM W22241, Olive R.; *Normanby R Basin*: QM W4001, Hann R., c. 112 km NW of Cooktown; QM W16691, Hann R. near Hann R. roadhouse; QM W11979, Kennedy R., Hann

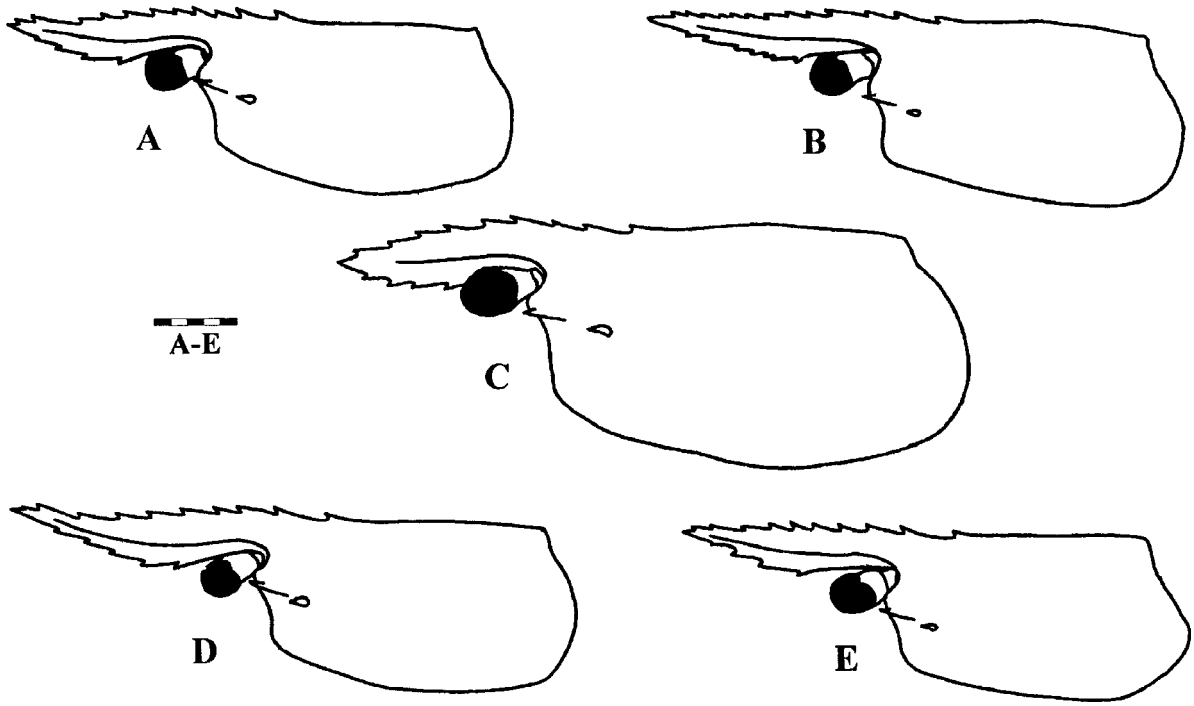

Figure 21. Rostrum variation within a single population of *Macrobrachium australiense* Holthuis, 1950, QM W14932, Thomson R. at Muttaburra, NW.Qld (type locality of *M. atactum sobrinum* Riek, 1951). (A) male 16.2 mm CL, (B) male 16.9 mm CL, (C) male 22.2 mm CL, (D) male 17.1 mm CL, (E) male 15.6 mm CL, Scale divisions 1 mm.

Crossing; QM W16902, Normanby R., Battle Camp-Cooktown Rd crossing; QM W16396, East Normanby R., c. 40 km SW of Cooktown; *Endeavour R Basin*: QM W19652, Endeavour R., 19 km NW of Cooktown; QM W5423, Annan R., Shiptons Flat; *Barron R Basin*: QM W19943, Jumrum Ck, crossing in Jumrum Environmental Park, off Barang St, Kuranda; QM W7986, Kuranda; QM W16636, Kuranda Ra., first creek on west side, Cairns-Kuranda Rd; QM W15502, Granite Ck, Walkamin; QM W19938, Rocky Ck, Kennedy Hwy bridge near Walkamin; *Mulgrave-Russell Rivers Basin*: QM W12588, Little Mulgrave R. near Gordonvale; QM W19806, Kearneys Ck; *Tully R – Dunk I Basin*: QM W19805, Tully R. catchment, unnamed creek; *Johnstone R Basin*: W19635, North Johnstone R.; W19260, Malanda Falls, North Johnstone R.; QM W19645, Utchee Ck; QM W19603, Victory Ck; QM W19637, Wadda Ck; QM W19644, Berner Ck; QM W19631, Dirran Ck; QM W19607, Duffer Ck; QM W19649, Ithaca R.; QM W19633, Mena Ck; QM W19626, Meuanbah Ck; QM W19622, North Beatrice R.; QM W19621, Ranken Ck; QM W19620, South Johnstone R.; QM W18728, Theresa Ck; QM W21491, Fisher Ck at Fisher Ck Rd bridge; *Tully R Basin*: QM W19805, Tully R. catchment, unnamed creek; *Herbert R Basin*: QM W17115, Millstream Ck, Allen Rd; QM W14685, Little Cedar Ck, Ravenshoe; QM W22182, Vine Ck near Ravenshoe; QM W22057, Little Cameron Ck, c. 2 km above Koombooloomba Rd crossing; QM W23123, Palm I.; *Murray R Basin*: QM W22149, Murray R. at Bruce Hwy crossing; *Ross R Basin*: QM W3024, Ross R. Weir, Townsville; QM W19956, Stuart Ck, behind Stuart Drive-in Theatre on Bruce Hwy; QM W21486, Alligator Ck below Bowling Green Bay N.P. near Townsville; *Haughton R Basin*: W18262, Reid R., bridge on Townsville-Charter Towers Rd; *Burdekin R Basin*: QM W18265, Eight Mile Ck, Charters Towers-Mt Garnet Rd crossing; W19946, Puzzle Ck tributary near Hidden Valley, Paluma Ra.; QM W12608, Running R., between Ewan and Hidden Valley; QM W18285, Plantation Ck, Ayr; QM W16625, Burdekin R., Echo

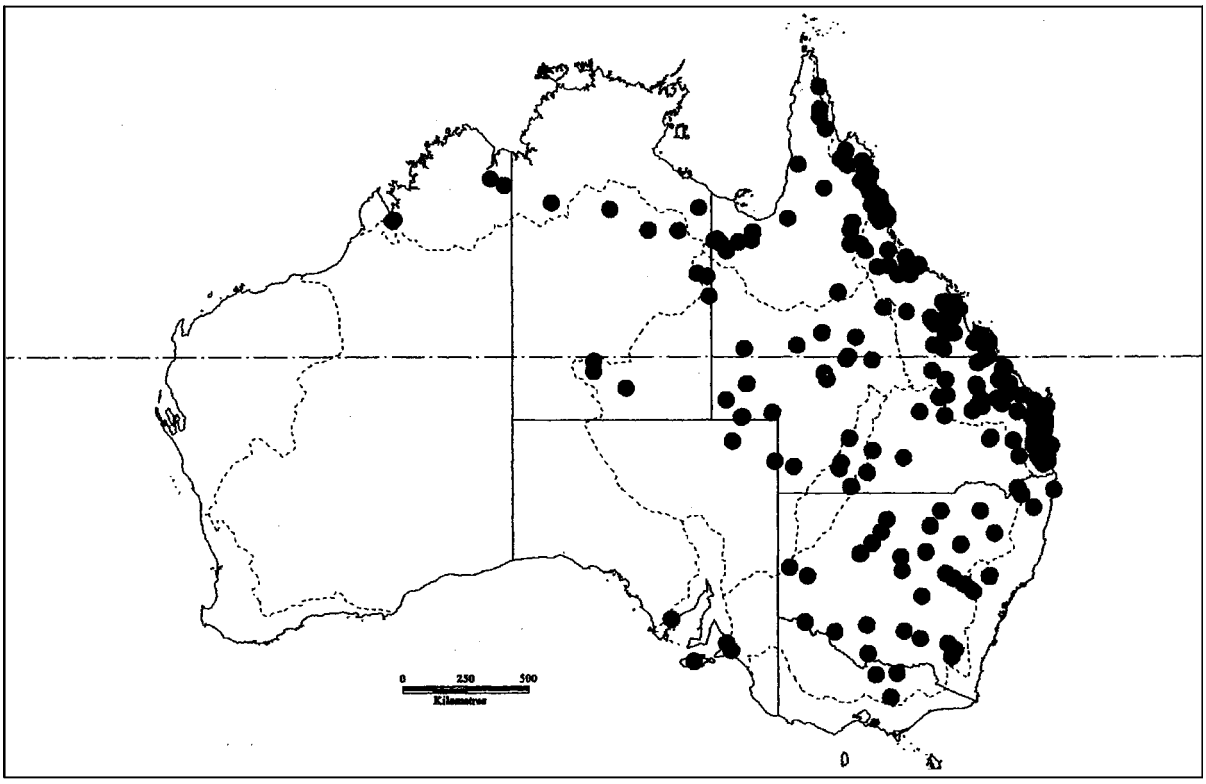

Figure 22. Distribution of *Macrobrachium australiense* Holthuis, 1950.

Hole, Charters Towers-Ravenshoe Rd; QM W8024, Burdekin R., Valley of Lagoons; QM W5040, Allingham Ck, Bluff Downs; QM W14894, Burdekin R., Macrossan; QM W11544, Burdekin R.; QM W4418, Eungella Dam; W17251, Broken R. tributary, Eungella N.P.; QM W14237, Belyando R., Mt Douglas; *Proserpine R Basin*: QM W22226, Palm Ck near Proserpine on Conway Ra. Rd; QM W22035, Saltwater Ck near Proserpine; *O'Connell R Basin*: QM W22079, Boundary Ck; QM W22153, Murray Ck, Rostirollas Rd crossing near Mt Ossa; QM W22192, Silent Grove Ck near Mt Ossa; *Pioneer R Basin*: QM W4788, Finchatton Ck, bottom of Finchatton Gorge, Finchatton; QM W8023, Balnagowan area, west of Mackay; QM W18260, Cattle Ck, last crossing on Mackay-Eungella Rd; QM W4798, Cattle Ck, Gargett; QM W4805, Pioneer R., Marian; *Plane Ck Basin*: QM W7992, Bells Ck, east of Sarina; QM W22031, Cab Ck near Inneston south of Sarina; QM W22203, Marion Ck, Ilbilbie, Bruce Hwy crossing; QM W22186, Sandy Ck, Homebush; *Shoalwater Ck Basin*: QM W19339, Wadallah Ck, Shoalwater Bay area; QM W19332, Boundary Lagoons on Stanage Bay Rd; *Fitzroy R Basin*: QM W4802, Nebo Ck, Collinsville Rd near Nebo; QM W4415, Eureka Ck near Goonyella mine; QM W4416, Eureka Ck, Isaac R. junction; QM W4786, Funnel Ck, off Bruce Hwy; QM W4414, Isaac R; QM W5088, Grahams Lagoon, Dipperu N.P.; QM W9739, Grosvenor Ck, junction with Isaac R; QM W8016, Connors R., 10 km upstream Bruce Hwy; QM W19336, Olive (=Stony) Ck, back road to the Isopod; QM W19937, Marlborough, creek beside Marlborough Caravan Park; QM W4410, Peak Downs;; QM W8026, Oakey Ck, 50 km east of Capella; QM W18255, Plentiful Ck, Bruce Hwy crossing near Yaamba; QM W12589, Yeppen Lagoon, Rockhampton; QM W12591, Neerkol Ck, between Rockhampton and Stanwell; QM W16394, Neerkol Ck, Stanwell; QM W8018, Fitzroy R., north of Gogango; QM W12599, Carnarvon; QM W19947, Carnarvon Ck, crossing near Early Storms; QM W12598, Dry Ck, Kroombit Tops; QM W19948, Kroombit Ck, beside forestry; QM W8021, Comet

R., 15 km north of Rolleston; QM W4413, Moura, water supply dam (central); QM W8025, Lake Nuga Nuga, NW side; QM W7987, Dawson R., junction with Delusion Ck; QM W7989, Dawson R., Kianga, above Moura Weir; QM W7990, Dawson R., Glebe Weir; QM W19957, Dawson R.; QM W7991, Baffle Ck, Injune area; *Calliope R Basin*: QM W7876, Gladstone, creek at Sunvalley; QM W16419, Calliope R. near Gladstone; *Boyne R Basin*: QM W7995, Briffney Ck, Gladstone; QM W4781, Granite Ck, foot of Bulburin S.F; QM W4398, Bulburin S.F; QM W4809, Bulburin S.F. near No.1 forestry camp; QM W4796, Boyne R., Nevertire Crossing near Builyan; *Burnett R Basin*: QM W4417, Nogo R., below Wurumba Dam; QM W4006, Wurumba Dam, Nogo and Burnett Rivers; QM W20736, Burnett R., Yarrol Stn, east of Monto; QM W19662, Eidsvold; QM W8005, Ban Ban Springs; *Burrum R Basin*: QM W17971, Elliott R., Goodwood-Bundaberg Rd bridge; QM W17966, Gregory R., Childers-Goodwood Rd bridge; QM W12603, Gregory R., Childers area; QM W14893, Burrum River Hatcheries; *Mary R Basin*: QM W7997, Tinana Ck; W16422, Mary R., Tiaro; QM W16426, Mary R. near Miva; QM W7998, Coondoo Ck-Tinana Ck; QM W19939, Six Mile Ck, Cooran; QM W3838, Amamoor Ck tributary near Gympie; QM W3194, Yabba Ck near Kenilworth; W19955, Booloumba Ck; QM W14896, Mary R., Conondale; QM W11843, Obi Obi Ck near Maleny; *Fraser Island Basin*: QM W11861, Lake Wabby, Fraser I.; *Noosa R Basin*: QM W4191, Searys Ck, Cooloola; QM W5090, Noosa R., Cooloola; *Maroochy R – Bribie I Basin*: QM W19601, Mooloolah R., bridge on Stevens Rd; QM W16580, Six Mile Ck, Elimbah; *Pine R Basin*: QM W20005, Burpengary Ck at Oakey Flat Rd crossing; QM W4409, North Pine R., above Pine Ck junction; QM W4420, Terrors Ck; QM W4406, Mt Sampson Ck; QM W19942, Cedar Ck, second last culvert on Cedar Ck Rd; QM W7293, Cabbage Tree Ck; QM W1174, Downfall Ck, Chermside; W7285, Nundah Ck; QM W7291, Schultz Canal near railway line; W15670, Kedron Brook, Kalinga Park; QM W7280, Kedron Brook, Kedron Sports Club; W14895, Kedron Brook, Toombul Overpass; *Stradbroke – Moreton Islands Basin*: QM W20603, Ben Ewa Ck, c. 1 km north of Tangalooma, Moreton I; *Brisbane R Basin*: QM W1870, Kilcoy Ck; QM W6538, Somerset Dam; QM W9984, Enoggera Ck, above Enoggera Dam; QM W16525, Enoggera Ck near bridge on Payne Rd, The Gap; QM W7283, Enoggera Ck; QM W1867, West Ithaca Ck, Mt Cootha; QM W14897, Ithaca Ck, Bowman Park; QM W15952, Moggill Ck, Brookfield; QM W7294, Moggill Ck tributary, Brisbane; QM W19952, Hayes Ck, off Moggill; QM W16407, Norman Ck, Ekibin Reserve; QM W16405, Norman Ck, Turbo Drive, Coorparoo; QM W12606, Brisbane R., Sapling Pocket near Lake Manchester; QM W7994, Brisbane R., Colleges Crossing; QM W7275, Goodna Ck, via Redbank; QM W7295, Indooroopilly near Indooroopilly bridge; QM W7282, Blunder Ck, Coopers Plains, Brisbane; *Logan-Albert Rivers Basin*: QM W12618, Leslie Harrison Dam; QM W11990, Albert R., Dunnes Crossing; QM W4641, Logan R., Lindsay Hwy crossing; *Richmond R Basin*: AM P13175, Duck Ck; *Clarence R Basin*: QM W19581, Mann R., Hanging Rock property, via Jackadgery; QM W21875, Chandlers Ck at Opossum Ck Rd; *Hunter R Basin*: QM W21897, Jerrys Plains, Hunter R.

Lake Eyre Drainage Region. NTM Cr007384, Lorne Waterhole, Lorne; SAM C5851, Ranken R., Barkly Tableland; NTM Cr007268, Rankin R., Long Eura Waterhole; NTM Cr007389, James R., Four Mile Hole; NTM Cr007326, Georgina R., Junction Waterhole; NTM Cr007267, Georgina R.; NTM Cr002152, Dead Dog Waterhole; NTM Cr010260, Alice Springs area, between Lake Nash Stn hmstd and Alpurrurulam Community; QM W14582, Georgina R., Pasapiturie Hole, Wirrilyerna Stn; QM W9990, Cluny; QM W19936, Western R., c. 1.5 km from Winton at Jundah; QM W19954, Western R., Cragg Family Bridge, Jundah Rd; QM W19573, Diamantina R., Old Cork Stn hmstd; QM W7276, Lake Muncoonie, 80 km NW of Birdsville; SAM C5852, Gilmour Ck, Birdsville-Bedourie Rd; QM W9992, Betoota; QM W9993, Diamantina R., Birdsville; QM W9994, Goyden Lagoon; QM W11965, Mogga Ck, tributary of Lake Buchanan; QM W14932, Thomson R., Stonehenge; QM W19951, Longreach Waterhole, Longreach-Winton Rd, 1.5 km from Longreach; QM W19953, Lagoon Ck, Barcaldine; QM W17171, Vergemont Ck; QM W17475, Barcoo R., Tambo; AM P18552, Cooper Ck, c. 16 km east of Innaminka; NTM Cr002106, Ormiston Gorge Reserve, main waterhole; NTM Cr000241, Ormiston Gorge; NTM Cr002113,

Ormiston Ck; NTM Cr002339, Macdonnell Ranges; SAM C5853, near Hugh R.; SAM C5854, Carpamoongana Waterhole, The Hamilton.

Bulloo-Bancannia Drainage Region. QM W10911, Boolbanna Stn on Thargomindah-Quilpie Rd; QM W10902, Yappi Ck, Norley Stn, north of Thargomindah; QM W7286, Thargomindah.

Murray-Darling Drainage Region. QM W17112, Paroo R., Eulo near bridge; QM W20677, Paroo R., Spring Ck Stn; QM W20674, Spring Ck Stn near Paroo R; QM W17111, Lake Numalla, SW of Eulo; QM W3814, Condamine R. Weir, Chinchilla; QM W12596, Condamine R., west of Chinchilla; QM W12623, Gowrie Ck, west of Toowoomba; QM W14933, Ballandean; QM W9138, Bald Rock Ck, Girraween N.P.; QM W16494, Accommodation Ck near Bald Mountain; AM P12347, Tenterfield; AM P12238, Bourke; AM P18554, Darling R. and billabongs near outlet from Lake Menindee; AM P26894, Namoi R., upstream from Manilla; AM P11857, Macquarie R., Dubbo; AM P13290, Goodradigley R., Wee Jasper; NTM Cr009845, Murrumbidgee R., Balranald; AM P12255, Murrumbidgee R.; AM P12254, Cotter R.; NMV J21498, Murray R., Mildura; NMV J21496, Goulbourn R., Mooroopna; QM W19574, Murray R., Younghusband; SAM C5857, Angas R., Strathalbyn; SAM C5855, Lake Alexandrina, Milang.

South Australian Gulf Drainage Region. SAM C5856, Eyre Peninsula.

Western Plateau Drainage Region. *unco-ordinated* streams: NTM Cr007387, Newcastle Ck, Mundah Waterhole; NTM Cr002124, Longreach Billabong near; NTM Cr006181, Long Waterhole, Vesswell Stn; NTM Cr006180, Adder Waterhole, Anthony Lagoon Stn.

Diagnosis

Rostrum. Short to medium length in fully developed males, developmental range 0.5–1.3 CL; moderately deep (maximum depth slightly more than dorsoventral diameter of eye); dorsal carina convex, straight, or slightly sigmoidal, rarely upturned, dentate along entire length, teeth subequally spaced, 6–12 teeth, 1–3 completely postorbital, one or more proximal teeth submoveable (incomplete basal suture) in fully developed males; ventral carina dentate, 2–6 teeth, first tooth located in proximal half or at about midlength.

General cephalon. Ocular cornea large, well-pigmented, accessory pigment spot present. Inferior orbit moderately produced, obtuse, postantennular carapace margin evenly rounded. Bec ocellaire moderately developed. Scaphocerite stout, c. 3 times maximum breadth, lamina distinctly tapering from broadest point to anterior margin (sometimes with lateral and mesial margins subparallel in adults), anterior margin produced forward at inner angle or less commonly evenly rounded, not strongly produced forward at midline. Epistome completely divided into two lobes, lobes rounded.

Mouthparts. Third maxilliped terminal segment clearly shorter than penultimate segment; exopod slightly shorter than ischiomerus. Mandibular molar process crowns as figured (Fig. 19D).

Second chelipeds (fully developed male). Larger and more developed than female P2; isomorphic in setation and shape, distinctly unequal in length; long, merus of minor cheliped reaching distal end of scaphocerite; bearing simple, protective and pappose setae; all segments except fingers with abundant well spaced, erect, mamilliform protective setae; pappose setae forming thick pubescence on fingers; simple setae few and scattered; fingers with well developed gape; pollex of moderate length, not noticeably broadened basally, about equal in breadth to basal dactylus, dactylus of moderate length, about equal in length to clearly shorter than manus, proximal cutting edges highly variable, often with both fingers bearing two large teeth (sometimes compound) separated by distinct gap, those on dactylus slightly advanced of those on pollex, proximal tooth on dactylus often distinctly hooked backwards, distal cutting edges crenulate; manus subcylindrical, occasionally inflated, maximum breadth slightly greater than to c. equal to maximum merus breadth, clearly longer to about equal in length to dactylus; carpus much shorter than chela, elongated, tapered, occasionally subdistally inflated; merus c. equal in length to slightly longer than carpus, tapered; ischium tapering proximally, compressed, narrowest point subproximal, with shallow median depression on superior face.

Third pereiopods (fully developed male). Short, dactylus reaching distal end of scaphocerite; lack-

ing protective setation; dactylus elongated, length more than four times basal breadth, ventral carina well developed, strongest at base of unguis; unguis moderately developed, about one quarter length of remainder of dactylus.

Thoracic sternum. T4 with well-developed median process, postcoxal flanges situated posterior to and distinct from median process. Developed male T8 with anterolateral lobes widely separated posteromedially, without median process posteriorly.

Abdomen. Inter-uropodal sclerite with moderately-developed, low, rounded pre-anal carina (often poorly developed in young specimens). Distolateral process on uropodal exopod with accessory spiniform seta mesially.

Body setation (fully developed male). Protective setation absent on carapace and abdomen.

Colour

Antennal flagella translucent, slightly tinged with olive or brown, peduncles olive brown, scaphocerites blue grey. Rostrum translucent with olive to olive green specks to uniform olive grey. Ocular peduncles light olive grey specked with olive to olive green. Base colour of body light olive grey with numerous specks of olive to olive green, specks generally covering most of abdomen but forming large irregular blotches on lateral carapace, specks more extensive on dorsal carapace. Carapace blotches less extensive but more distinct in females and developing males, some fully developed males uniformly dark brown on carapace. Tail fan strongly tinged with blue-grey distally.

Ambulatory legs marked with light orange at joints of segments, otherwise with indistinct brown to grey transverse bands or light orange specks. Base colour of second chelipeds olive grey to light grey brown, overlaid with reticulated markings, fingers and fingertips always dark brown but covered with lighter tan-coloured pubescence in fully developed males, fully developed males generally striped with slightly irregular dark olive brown longitudinal bands running length of chelipeds (in developing males bands often irregular and discontinuous over length of chelipeds).

Developing ova olive green.

Specimens from inland populations in highly turbid water are usually translucent pinkish cream with poorly developed chromatophore patterning.

Life cycle

Adults predominantly in fresh waters, sometimes extending into low salinity brackish waters up to 2 ppt salinity, tolerant of salinities up to 17.5 ppt in laboratory studies (Denne, 1968), larval development abbreviated, three planktonic stages, metamorphosis occurring in 4–9 days in fresh water in temperature range 20–30 °C (Fielder, 1970; Kneipp, 1979), survival high in salinities up to 15–16 ppt (Lee & Fielder, 1981; Kneipp, 1979), survival markedly reduced (3% survival) in seawater (Kneipp, 1979); positively rheotactic (Lee & Fielder, 1984), mass upstream migration and climbing behaviour observed at Glebe Weir on the Dawson River by Lee & Fielder (1979); ovigerous females observed rafting on mats of macrophytic debris during wet season floods near the mouth of the Johnstone River (W. Lee Long pers. com.); eggs moderately large and few, 38–197 per brood (Kneipp, 1979), maximum length of developed ova, 1.4 mm.

Size

Medium-sized species. Maximum size of developed male 27 mm CL, 91 mm TL. Maximum size of female 20 mm CL, 71 mm TL, minimum size of ovigerous female, 5.8 mm CL.

Habitat ecology

A highly adaptable species occurring in a wide variety of habitats: perennially flowing creeks, rivers and plateau streams; waterholes, billabongs, lagoons and lakes on episodic and seasonal watercourses; man-made lakes, reservoirs and artificial drains; offshore sand islands (Lake Wabby, Fraser Island and Ben Ewa Ck, Moreton Island) and offshore continental islands (Palm Island). This is the only species to have colonised endorheic catchments and the dry interior of the continent. The altitudinal distribution of the species extends from near sea level to upper catch-

ment headwaters, plateaus and highlands (up to 900 m elevation). Substrates: fine to coarse particle size, including bedrock. Flow: zero to high, 0–100 cm/s with a preference for low flow conditions <40 cm/s reported by Kneipp (1979). Preference for low flow habitats further supported by positive rheotactic response recorded by Lee & Fielder (1984). Water clarity: low to high. Water depth: mostly from 0.3 to 2.0 m. Recorded physico-chemical tolerances: water temperature 15.9–33 °C (field, this study $n = 24$; Kneipp, 1979, $n > 100$), DO_2 4.0–11.0 ppm (field, $n = 37$) or 2 ppm minimum (with 100% survival to 96 h) in the laboratory at 30 °C (Kneipp, 1979), pH 6.0–8.0 (field, $n = 49$), hardness <10–320 ppm (field, $n = 27$). Fringing vegetation: open communities dominated by *Eucalyptus*, *Melaleuca*, *Casuarina*, and *Pandanus* to closed monsoonal forest and rainforest, anthropogenically disturbed areas.

Behaviour

In clear water, adults are mostly nocturnal and prefer to shelter during daylight in well-shaded areas underneath fallen timber, overhanging banks, boulders, rock ledges, or in deep leaf litter beds. Juveniles are commonly found among macrophytes or in leaf litter beds. In highly turbid inland waters sheltering behaviour is less developed during daylight and the second pereiopods of feeding adults may be seen breaking the surface of the water. General behaviour of this species has been well studied – maintenance and reproductive behaviour by Ruello et al. (1973) and Lee & Fielder (1982); agonistic behaviour and dominance hierarchies by Lee & Fielder (1983).

Distribution

Eastern, inland and northern Australia. Northern Drainage Region (disjunct distribution): Fitzroy R. basin, W.A. to Victoria R. basin, N.T. and Calvert R. basin, N.T. to the Wenlock R. basin, Qld; Eastern Drainage Region: Olive-Pascoe Rivers basin, Qld to Hunter R. basin, N.S.W; Western Plateau Drainage Region; Lake Eyre Drainage Region; Bulloo-Bancannia Drainage Region; Murray-Darling Drainage Region.

Systematic position

The relationship of *M. australiense* to other Australian taxa is presently unclear. The species shows superficial resemblance to *M. equidens*, *M. bullatum* and *M. idae* but it differs in having a rounded inferior orbit (vs. angular) and the merus of P2 about equal in length to the carpus (vs. clearly shorter than the carpus) in developed males.

Young males and females of *M. tolmerum* can also be confused with the species but differ in having a keel-like, strongly elevated pre-anal carina vs. a low, rounded carina in *M. australiense*. The fingers of P2 are also much shorter in young *M. tolmerum*, being c. half as long as the manus or less whereas in *M. australiense* the fingers are almost as long as the manus in young specimens.

Vernacular names

Common Australian river prawn.

Remarks

This is by far the most wide-ranging and common Australian species, occurring over almost half the continent. A highly adaptable prawn, it survives in a wide variety of climatic conditions.

M. australiense was known in the early literature as *Palaemon australis* Ortmann, 1891, a name pre-occupied by *Palaemon australis* Guérin-Méneville, 1838. Holthuis (1950) provided the replacement name, *Macrobrachium australiense*.

Ortmann's type series consisted of a series of specimens from Gayndah, Peak Downs and Rockhampton, eastern Qld and was deposited in the Strasbourg Museum. The type material was not available for this study.

The species provisionally assigned to *M. australiense* by Holthuis (1950) and originally reported by De Man (1888a: 711; from the collection of the Göttingen Museum) as *Palaemon* n.sp? from Sydney, N.S.W., differs significantly in having the merus of the second pereiopods clearly shorter than the carpus (McNeill, 1929). The species is most likely *M. equidens* (Dana). Similarly, the specimen from Sydney (possibly an erroneous locality) reported by Holthuis (1950) agrees closely

with *M. equidens* and lacks the low pre-anal carina on the inter-uropodal sclerite, has an angular inferior orbit and is larger in size than typical for this species (see *M. equidens*).

Palaemon ornatus Baker, 1914, reported from Hermannsburg, N.T., and Running Waters based on 'one larva', in all probability belongs with this species, as this is the only *Macrobrachium* occurring in inland endorheic streams in Australia.

The record of *Palaemon australis* from the Katherine River, N.T. by Roux (1933) is more likely *M. bullatum* Fincham.

McNeill (1929) provided a thorough redescription of the species (as *Palaemon* (*P.*) *australis* Ortmann) based on a large series of specimens from the Horton River at Pallal, N.S.W. Although McNeill noted a high degree of geographic variation he warned of the pitfalls of describing new forms without an adequate appraisal of variation within populations:

'It appears that *Palaemon* (*P.*) *australis* has a most extensive range in the freshwater river systems of the eastern and southern portions of Australia, and that many perplexing racial forms exist similar to those exhibited by the Australian freshwater atyid shrimp *Paratya australiensis* Kemp. Possibly varieties of the species also occur. Unfortunately, however, our present material is meagre, and it is practically useless to base descriptions on anything but complete series of specimens from individual localities as in the present instance.'

Despite McNeill's cautionary comments, Riek (1951) erected four subspecies from a limited number of localities:

M. australiense australiense – Gayndah, Rockhampton, Peak Downs (type localities); Enoggera Ck, Brisbane.
M. australiense eupharum – Burdekin R; Rosewood.
M. australiense cristatum – Horton R. (McNeill's variety); Johnstone R; Bourke; Narrabri; junction of Namoi and Barwon Rivers; Deniliquin; Broken Hill; Collarenebri; Riverina District; Cotter R; Murrumbidgee R.
M. australiense crassum – Cairns; Kuranda.

These subspecies appear to have been based largely on the shape of the rostrum and the relative length and breadth of the carpus of the second pereiopods. Lee (1979) in a study on the status of these sub-species in a Ph.D. thesis, concluded that the differences between subspecies described by Riek, 'do not appear to be sufficiently large or consistent enough to warrant dividing the species into 4 subspecies'.

An examination of over 1700 specimens in this study revealed a high degree of geographic variation in rostrum shape. Populations from neighbouring drainage basins often showed quite a degree of difference (Fig. 20). There is also considerable developmental variation in the shape of the rostrum. Fully developed males tend to have a shorter more convex rostrum. The relative length and breadth of the carpus also shows considerable developmental variation, as is typical for other species of the genus (Henderson & Matthai, 1910; Cowles, 1914; Holthuis, 1950; Kuris et al., 1987).

Although there is considerable geographic variation in rostral features it is not obviously clinal. Long rostrum populations occur on Cape York Peninsula to as far south as the Barron River on the northeast coast, are common through the western Gulf of Carpentaria streams and the Lake Eyre drainage division, but occur again on the east coast in the Burrum R. basin in southeast Queensland. Populations from the Johnstone, Herbert and Burdekin Rivers differ from other northern forms in having a short rostrum and are similar in this regard to Murray-Darling populations. It is therefore difficult to delimit subspecies and link them to definite geographic areas based on rostral features.

Available data on the life cycle of this species suggest that it is largely land-locked in the numerous drainage basins throughout its range. Some gene flow may occur between adjacent exorheic catchments by way of freshwater plumes during episodes of high freshwater outflow. In general, along shore dispersal is likely to be very limited. Although there is undoubtedly morphological divergence between catchments and across the broad geographic range of the species, delimiting subspecies is likely to be a difficult and impractical task, considering the large number of drainage basins involved. At this point in time it is hard to justify the continued usage of Riek's subspecies or to describe further subspecific taxa.

Using allozyme and molecular data, Cook et al. (2002) studied dispersal patterns in four of the major inland drainage catchments – the Darling, Cooper, Bulloo and Diamantina. Large and significant levels of allozyme and mtDNA differentiation were found between catchments, indicating limited gene flow in recent times. By contrast, *M. australiense* was found to be panmictic within catchments.

The nominal taxa, *M. adscitum adscitum*, *M. atactum atactum* and *M. atactum ischnomorphum* described by Riek (1951), all fall within the range of variation of this species. The holotype of *M. atactum atactum* is a large developing male – the pappose setal pubescence and proximal teeth on the fingers of the second chelae are not fully developed. Similarly, the holotype of *M. atactum ischnomorphum* is a large male with developing chelipeds – protective setae are small, sparsely distributed and sharp; the proximal teeth on the cutting edges are small with the distal median lamella remaining, the fingers are longer than the manus etc.

M. adscitum adscitum is also based on a developing male – one second pereiopod is undeveloped (possibly regenerated) and the other sub-developed. The distal cutting edges of the fingers of the sub-developed cheliped are characteristically crenulated. The rostrum is somewhat aberrant in being deep for its length but the rostral formula falls within the range of *M. australiense*. The relatively inflated manus described as characteristic of *M. adscitum adscitum* by Riek is a common feature of undeveloped and sub-developed chelae in many species.

The holotype of *M. atactum sobrinum* Riek, is a developed male with a long rostrum (typical of many western and northern populations). The specimen is aberrant in having an epigastric tooth but otherwise falls within the range of variation of *M. australiense*.

Further support that *M. australiense* is the only species occurring in inland Australia is provided by a recent molecular study using nucleotide sequences from the 16S rRNA mitochondrial gene region (Murphy et al., in press). The degree of variation found between 16S haplotypes representing 12 different populations of '*M. australiense*' from a wide geographic area of central and eastern Australia was much less than that found between four other Australian species, viz. *M. rosenbergii* (De Man, 1879), *M. novaehollandiae* (De Man, 1908), *M. lar* (Fabricius, 1798) and *M. tolmerum* Riek, 1951. The haplotypes recognised contained ten variable sites with no insertions or deletions and showed 0.2 to 1.6% divergence whereas divergence levels amongst the four other Australian species ranged from 8.4 to 13.4%.

The aquaculture potential of *M. australiense* has been discussed by Fielder (1983) and growth and biogenics by Hewitt (1984). The species has been commercially harvested for fishing bait in Wivenhoe Dam in the Brisbane River valley (Beumer, 1990).

Macrobrachium koombooloomba sp. nov. (Figs 23, 24, 36A, 37C, D)

Macrobrachium sp. Short, 2000, p. 65.

Material examined

Holotype: *Eastern Drainage Region*. *Tully R Basin*: QM W22071, 1 male (fully developed), 19.6 mm CL, Koombooloomba area, creek on Koombooloomba Rd near Koombooloomba Dam turnoff, 17° 50′ S, 145° 34′ E, 10/6/1997, J. Short, A. Humpherys.

PARATYPES. *Eastern Drainage Region*. *Tully R Basin*: QM W24681, 1 male, CL 11.0, 3 females, CL 10.4–11.7 mm, same collection data as holotype; QM W22194, 1 male, CL 17.5 mm, Koombooloomba area, June 1997, J. Short; QM W22-045, 3 males (largest fully developed), CL 15.1–21.3 mm, 2 females, CL 10.1–12.9 mm, O'Leary Ck tributary below concrete causeway at Culpa Rd cr-ossing, 17°57′S, 145°38′E, 10-11/6/1997, J. Short, A. Humpherys; QM W18128, 1 male, CL 18.8 mm, same locality, 7/11/1992, J. Short, P. Davie; QM W18129, 1 male, CL 22.0 mm, same locality; QM W18130, 11 males, CL 5.8–16.2 mm, 4 ovig. fema-les, CL 11.1–13.7 mm, 2 females, CL 7.3, 14.0 mm, same locality; QM W18119, 8 males, CL 7.5–16.9 mm, 3 ovig. females, CL 12.0–13.6 mm, same loc-ality; QM W18132, 1 male, CL 18.3 mm, same loc-ality; QM W18126, 18 males, CL 5.4–14.8 mm, 8 ovig. females, CL 9.5–13.4 mm, 9 females, CL 5.7–8.3 mm, Tully R. near Old Culpa, 17°55′S, 145°37′

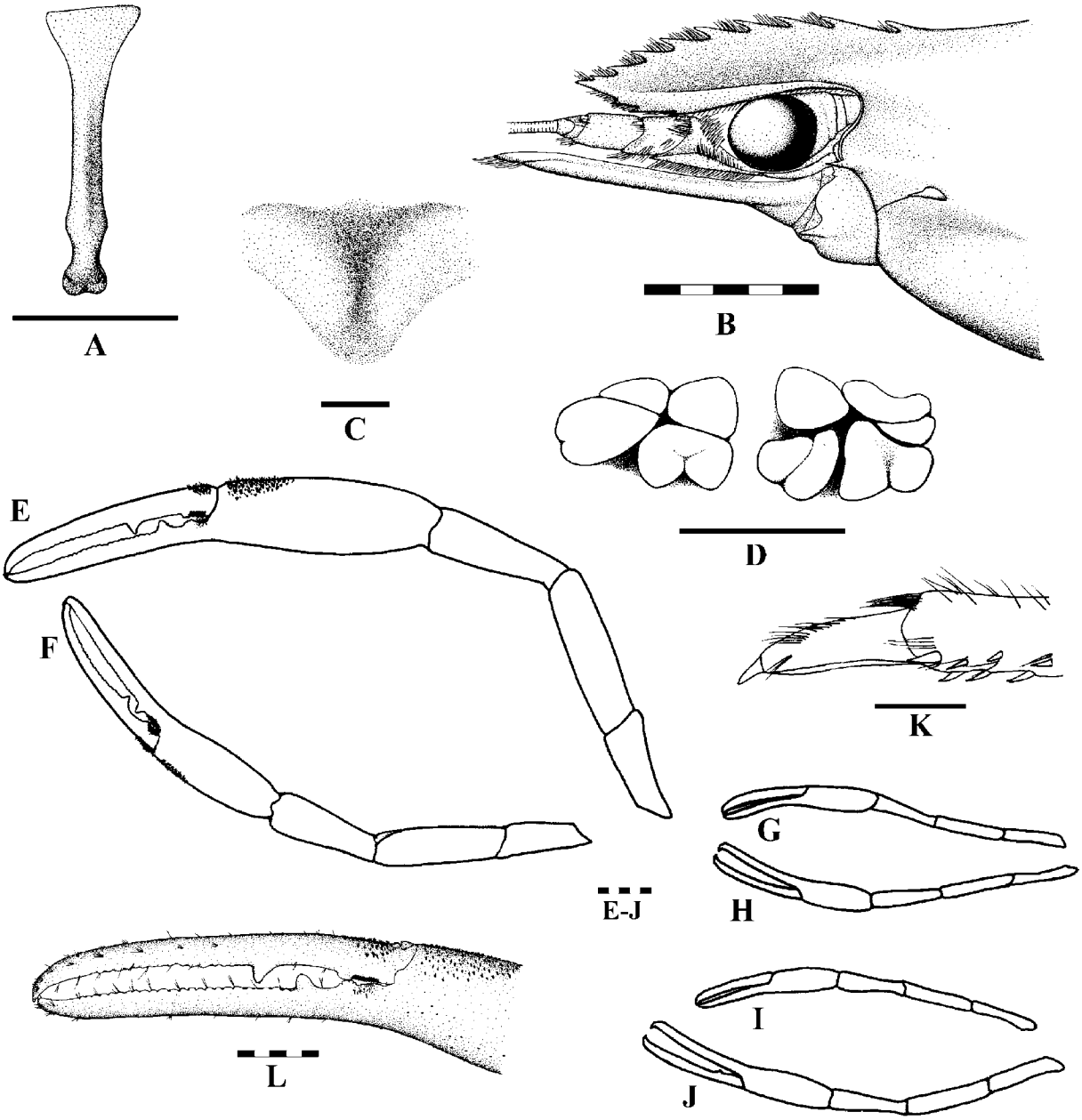

Figure 23. Macrobrachium koombooloomba sp. nov. (A) QM W18130, male paratype 15.9 mm CL, ventral view of inter-uropodal sclerite, (B) QM W18126, male paratype 14.8 mm CL, anterior cephalothorax, (C) QM W18130, male paratype 15.9 mm CL, epistome, (D) crowns of left and right mandibular molar processes (setae omitted) of same, (E) QM W22071, male holotype 19.6 mm CL, fully developed major second cheliped (protective setation omitted), (F) fully developed minor second cheliped (protective setation omitted), QM W18130, male paratype 16.0 mm CL, (G) undeveloped minor second cheliped (protective setation omitted), (H) undeveloped major second cheliped (protective setation omitted), (I) QM W18119, ovigerous female paratype 13.6 mm CL, minor second cheliped, (J) major second cheliped, (K) QM W22071, male holotype 19.6 mm CL, dactylus and distal propodus of fully developed right third pereiopod, (L) fingers and distal manus of fully developed right cheliped. Solid scale bars and divisions on divided scale bars 1 mm.

E, 7/11/1992, J. Short, P. Davie; QM W18122, 7 females, CL 7.2–9.3 mm, same locality; QM W18-117, 15 males, CL 5.1–14.2 mm, 3 ovig. females, CL 7.1–10.2 mm, females, CL 6.5–

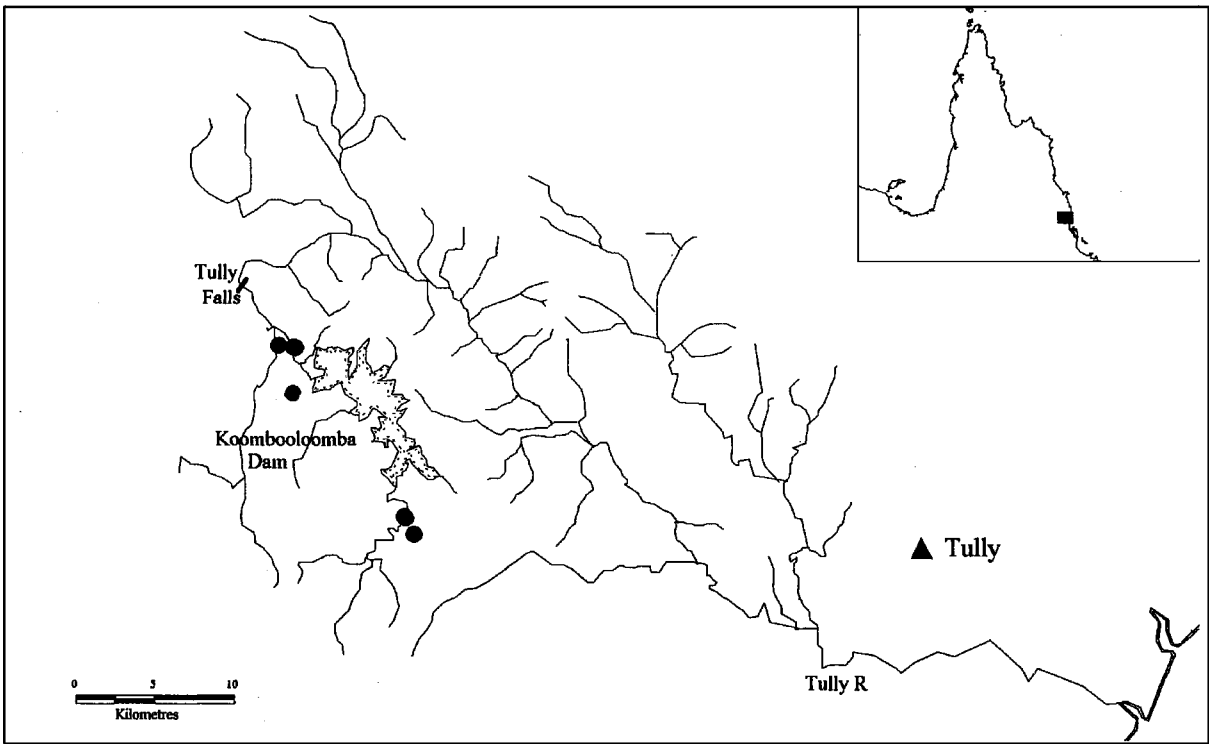

Figure 24. Distribution of *Macrobrachium koombooloomba* sp. nov.

10.8 mm, Nitchaga Ck, Koombooloomba Dam Rd crossing, 17°49′S, 145°33′E, 5–6/11/1992, J. Short, P. Davie.

Additional material. Tully R Basin: QM W17113, 3 ovig. females, CL 7.9–10.6 mm, 1 female, CL 9.6 mm, Tully R., between Tully Falls and Koombooloomba, 4/12/1990, S. Bunn, M. Bray; QM W17114, 2 males, CL 7.6, 8.3 mm, 1 female, CL 7.5 mm, Tully R., above Koombooloomba Dam, 28/11/1990, S. Bunn, M. Bray.

Description

Rostrum. Short, 0.55 CL (0.5–0.7 in paratypes); moderately deep (maximum depth about equal to dorsoventral diameter of eye); dorsal carina distinctly convex, dentate along entire length, teeth more closely spaced apically, otherwise subequally spaced, 8 teeth (7–10 in paratypes), 1 tooth completely postorbital, number of teeth along proximal margin submoveable; ventral carina unarmed for c. proximal two thirds of length, bearing 3 teeth (2–5 in paratypes).

General cephalon. Carapace spination reduced, hepatic spine feeble (broken off on one side in several paratypes), antennal spine small. Ocular cornea large, well-pigmented, accessory pigment spot present. Inferior orbit moderately produced, obtuse, postantennular carapace margin evenly rounded. Bec ocellaire moderately developed. Scaphocerite stout, length less than three times maximum breadth, lamina distinctly tapering from broadest point to anterior margin, anterior margin produced forward at inner angle. Epistome completely divided into two lobes, lobes rounded.

Mouthparts. Third maxilliped terminal segment clearly shorter than penultimate segment; exopod about equal in length to ischiomerus. Mandibular molar process crowns as figured (Fig. 23D).

Second chelipeds. Isomorphic in setation and shape, distinctly unequal in length; long, merus of minor cheliped reaching distal end of scaphocerite; bearing simple, pappose and protective setae; all segments except fingers with mamilliform protective setae, least developed on lateral and

mesial manus; fingers with few tufts of simple setae; base of dactylus with small sparse pubescence of pappose setae on superior face and cutting edge, similar pubescence on basal cutting edge of pollex, superior manus with more extensive, sparse pubescence distally; fingers with well developed gape, slender, slightly uncinate at tips, proximal cutting edges with pair of opposed molar teeth followed by distinct gap then pair of large incisor teeth, incisor tooth on dactylus more distal and directly strongly forward, distal two thirds of cutting edges crenulate; basal pollex not noticeably broadened, about equal in breadth to basal dactylus; maximum manus breadth much greater than maximum merus breadth, c. equal in length to dactylus (major cheliped) or clearly shorter than dactylus (minor cheliped); carpus much shorter than chela, elongated, tapered, slightly inflated subdistally; merus clearly longer than carpus, slightly inflated at mid-length, otherwise cylindrical; ischium compressed, tapered, with well developed median groove on superior face.

Third pereiopods. Short, dactylus reaching distal end of scaphocerite; lacking protective setation; dactylus stout, length less than three times basal breadth, ventral carina well developed; unguis poorly developed, a little less than one fifth remainder of dactylus.

Thoracic sternum. T4 without medial process. T8 with anterolateral lobes well separated posteromedially, well developed median process present posteriorly (poorly developed or indistinct in several paratypes).

Abdomen. Inter-uropodal sclerite slender, with low preanal carina (absent in juveniles and small adults paratypes). Distolateral process on uropodal exopod without accessory spiniform seta.

Body setation (fully developed male). Protective setation absent on carapace and abdomen.

Colour

Antennal flagella and scaphocerites translucent, tinged with olive grey. Peduncles greenish brown to light olive grey, mottled with blotches of olive grey to olive brown specks. Rostrum translucent, olive grey with specks of light olive brown to olive grey. Ocular peduncles translucent, olive grey to olive brown. Body mottled with irregular blotches of olive grey to olive brown specks on greenish brown to light olive grey base colour, tailfan slightly translucent specked with olive brown, lateral margin of uropodal exopods orange brown.

First chelipeds and ambulatory legs mottled with olive grey and lighter yellow grey, joints of segments and tips of dactyli tinged with orange brown. Second chelipeds mottled dark olive brown or olive on orange brown or olive yellow, finger tips generally orange brown, manus often with reticulated pattern.

Life cycle

Restricted to upper catchment fresh waters, eggs large and few, 5-92 ova per brood, maximum length of developed ova 1.9 mm. Larval cycle unstudied, large eggs and form of first larval stage indicative of highly abbreviated type. First larval stage large, robust, c. 5 mm total length; eyes sessile; rostrum downturned, entire; telson broad posteriorly with numerous plumose setae, uropods absent; five pairs of non-setose, short pleopods; all thoracopods present; maxillipeds with long natatory exopods, P1-4 with shorter non-setose exopods; P1-2 subchelate.

Size

Small species: Maximum size of developed male 22 mm CL, 65 mm TL. Maximum size of female 14 mm CL, 44 mm TL, minimum size of ovigerous female, 7 mm CL.

Habitat ecology

Restricted to permanently-flowing, upper catchment plateau streams at 650–750 m elevation. Substrates: Medium to coarse, including sand, gravel and rocks. Flow: zero to high. Water clarity: high. Water depth: 0.1–1.5 m. Recorded physico-chemical tolerances: water temperature 17–22 °C (field, $n = 12$), pH 5.5–6.8 (field, $n = 12$), hardness <20 ppm (field, $n = 12$). Fringing vegetation: rainforest (simple notophyll vine forest) grading into open eucalypt forest.

Behaviour

Shelters underneath fallen timber, boulders, rock ledges or in deep leaf litter beds.

Etymology

The specific epithet is an indigenous word from the Jirrbal language group derived from '*koomba*', old woman, and '*loomba*', other woman's place and refers to a secret place where women met (Girringun Elders and Reference Group Aboriginal Corporation, communicated via L. Pentecost and R. Smith). A water storage dam for the Tully Hydroelectricity Scheme, Lake Koombooloomba (also known as Koombooloomba Dam), was built in the vicinity in the late 1950's. Most of the present material of the new species, including the type locality, originates from the catchment of Lake Koombooloomba. The specific epithet is to be used as a noun in apposition.

Distribution

Upper Tully River basin, northeast Qld.

Systematic position

The new species shows a number of uncommon features for the genus – thoracic sternite 4 without median process; distolateral process on uropodal exopod without accessory spiniform seta and hepatic and antennal spines reduced. These features in combination with the large size of the ova and short rostrum suggest a lengthy period of geographic isolation. It is likely that the reduced spination is an adaptation to the high flow, upland habitat of the species.

Relationships between *M. koombooloomba* sp. nov. and other Australian species are obscure. In addition to the characters mentioned above, fully developed males of the new species also have a small patch of pappose setae on the distodorsal manus of P2. No other Australian species has pappose setae on the manus.

One character which suggests a possible link between the new species and *M. australiense* is the distally crenulate cutting edges on the fingers of P2 in developed males. However, this character also occurs in some unrelated American species.

Vernacular names

Koombooloomba prawn.

Remarks

This highly distinctive species is the most specialised of Australian river prawns and by far the most restricted. It is only known from upland streams in the upper Tully River catchment above Tully Falls at elevations between 650 and 750 m. These streams have permanent flow, fringing rainforest vegetation, and relatively cool water temperatures during summer (17–22 °C).

The new species was first collected by Dr Stuart Bunn and Mr M. Bray, Griffith University, during a limnological study for the proposed Tully-Millstream hydroelectric scheme in 1990. Material brought to the Queensland Museum for identification by Mr John Marshall, Griffith University, showed interesting features such as the large developed ova and unusual rostrum, indicating that it may be new to science. Queensland Museum expeditions to the area in November 1992 and June 1997 yielded numerous adult specimens, including several fully developed males.

Two other freshwater decapods endemic to the upper Tully River catchment have also been described by Short and Davie (1993), viz. the parastacid crayfish, *Cherax parvus* and *Euastacus yigara*.

Macrobrachium tolmerum Riek, 1951, (Figs 25, 26, 36E)

Macrobrachium tolmerum Riek, 1951, pp. 360 (key), 362 (in part), fig. 1. Short, 1995, p. 49. 2000, p. 63.

(?) *Macrobrachium danae* – Riek, 1951: 360 (in part, not Heller, 1865).

Material examined

Holotype. *Eastern Drainage Region. Black R Basin*: AM P11988, 1 female, CL, 18.3 mm [erroneously recorded as male by Riek, 1951], Black River, Macrossan [erroneous locality], E.F. Riek, October 1943.

Paratypes. AM P11990, 5 males, CL, 6.8–23.9 mm, 5 females, CL, 13.3–17.4 mm, same locality as holotype.

Northern Drainage Region. Buckingham R Basin: AM P11259, Yirrkala, Methodist Mission.

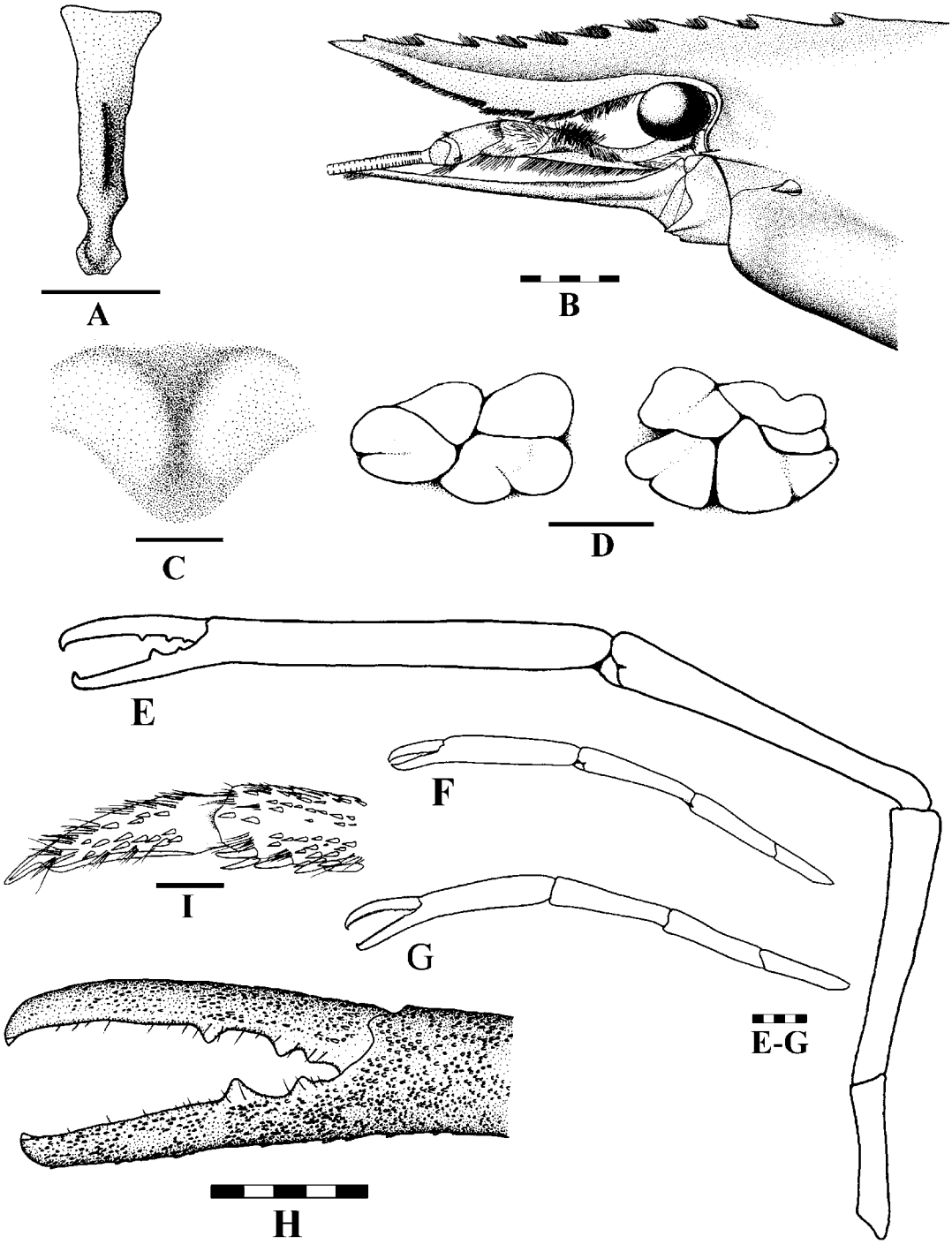

Figure 25. Macrobrachium tolmerum Riek, 1951. (A) QM W16628, male 22.4 mm CL, ventral view of inter-uropodal sclerite, (B) QM W5465, male 27.9 mm CL, anterior cephalothorax, (C) epistome of same, (D) crowns of left and right mandibular molar processes (setae omitted) of same, (E) QM W4552, male 25.8 mm CL, fully developed second cheliped (protective setation omitted), (F) QM W16800, male (16.0 mm CL), undeveloped second cheliped (protective setation omitted), (G) QM W19643, female 21.4 mm CL, second cheliped (protective setation omitted), (H) QM W4552, male 25.8 mm CL, fingers of fully developed second chela, (I) QM W5465, male 24.3 mm, dactylus and distal manus of fully developed left third pereiopod. Solid scale bars and divisions on divided scale bars 1 mm.

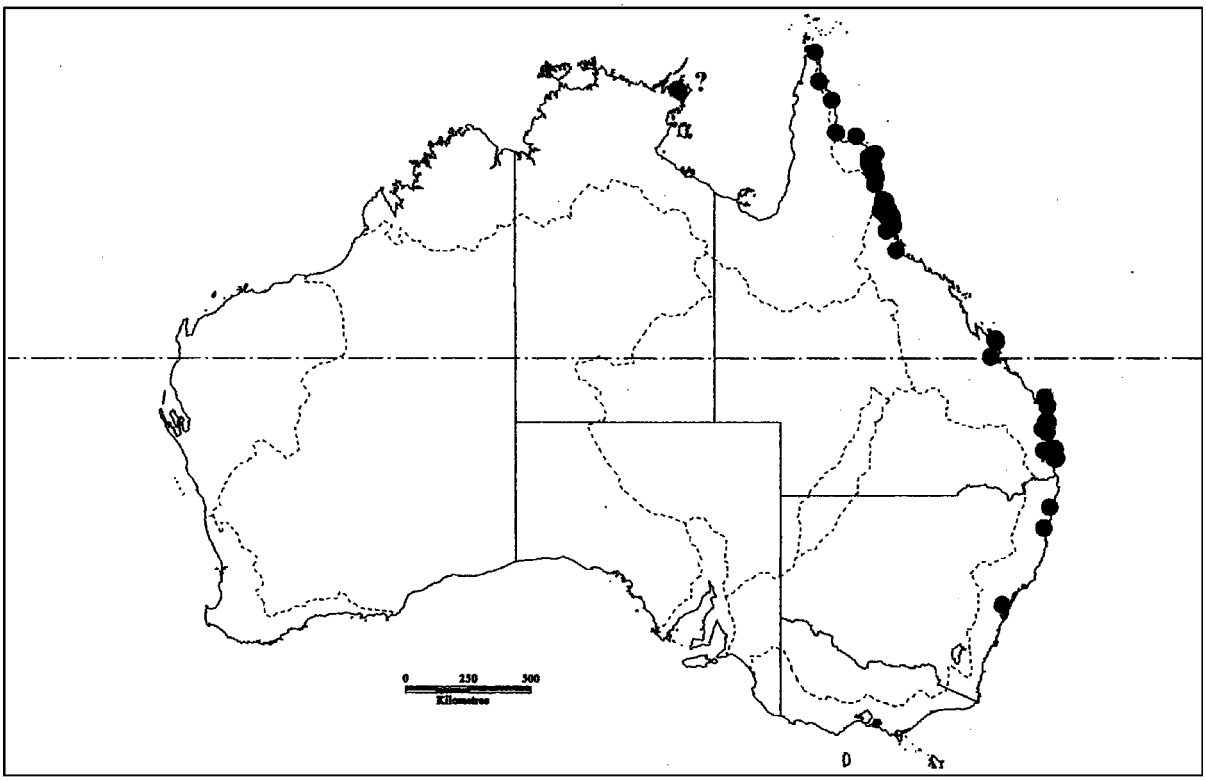

Figure 26. Distribution of *Macrobrachium tolmerum* (Riek, 1951)

Eastern Drainage Region. Jacky Jacky Ck Basin: AM P29514, Cape York, 30 km NE of Bamaga; QM W16800, *Nanthau Beach*; QM W16630, Harmer Ck, Shelburne Stn hmstd; *Olive-Pascoe Rivers Basin*: QM W22240, Olive R.; *Lockhardt R Basin*: QM W7300, Line Hill, Iron Ra.; *Stewart R Basin*: AM P13293, Stewart R.; QM W20053, Ronnie's Rocky Ck, Stewart R.; QM W20050, Stewart R., lower crossing; QM W21561, Rocky R., Silver Plains Stn; *Jeannie R Basin*: QM W20599, Cape Melville Ra., west side, water point; QM W17232, Arnies Lake, Cape Flattery; QM W17233, Windmill Lake, Cape Flattery; QM W18227, Cape Flattery, second creek south of headland; QM W17230, Cape Flattery; QM W18230, McIvor R., Isabella-McIvor Rd crossing; QM W20054, McIvor R., Mt Ray; *Endeavour R Basin*: QM W5420, Mt Cook N.P., west face of mountain; QM W16901, Isabella Ck, above Isabella Ck falls; QM W16898, north branch Endeavour R., Battle Camp-Cooktown Rd crossing; QM W5413, Endeavour R., 19 km NW Cooktown; QM W16905, Endeavour R., Jensens Crossing; QM W22041, Endeavour R. above first falls; QM W22054, Endeavour R. Right Branch, Cooktown-McIvor R. Rd crossing; QM W22022, Trevethan Ck, Cooktown Developmental Rd crossing; QM W5427, Annan R., Shiptons Flat; QM W5418, Parrot Ck, Shiptons Flat; *Daintree R Basin*: W5411, Russel Ck, Wyalla Plain, Bloomfield; QM W5415, Platypus Ck, Wyalla Plain, Bloomfield; QM W5412, Gap Ck, 12 mile Scrub, Bloomfield; QM W22077, Bloomfield R. below first falls; QM W19933, Daintree R., 2 km upstream of Daintree; *Barron R Basin*: QM W22213, Ellis Beach, north of Cairns, small creek; QM W16637, Stony Ck, Kamerunga; QM W17254, Freshwater Ck, Page Rd bridge, Genoma Park, Brinsmead; *Mulgrave-Russell Rivers Basin*: QM W7993, Moody Ck, Cairns; QM W7996, Gordon Ck, Woree, Cairns; QM W19950, Blackfellow Ck, Whereat St, Edmonton; QM W22051, Wright Ck at Bruce Hwy crossing; QM W19810, Kearneys Ck; QM W16628, Harvey Ck, Bellenden Ker; QM W22207, Josephine Ck, crossing on road to Josephine Falls; *Johnstone R Basin*: QM W22229,

Carmoo Ck, downstream of Tully-Mission Beach Rd crossing; QM W22075, Cowley Beach, creek on road to; QM W22235, Ella Bay, small creek c. 1.4 km north of Heath Park; QM W18274, Bamboo Ck mouth, Innisfail; QM W18277, North Bamboo Ck near Innisfail; QM W22012, Unnamed creek at Jubilee Grove estate, Innisfail; QM W22004, Unnamed creek near Innisfail; QM W19643, Berner Ck; QM W19605, Bora Ck; QM W19648, Cleminson Ck; QM W19608, Duffer Ck; QM W22047, Fishers Ck, road crossing above Gregory Falls; W19630, Horans Ck; QM W19629, Johnstone R.; QM W19611, Meingan Ck; QM W19639, Mena Ck; QM W19606, Miskin Ck; QM W19624, Ninds Ck; QM W22003, Headwaters of east branch of Ninds Ck; QM W19613, North Johnstone R.; QM W19646, Utchee Ck; QM W19602, Victory Ck; *Tully R – Dunk I Basin*: AM P2563, Dunk I.; *Murray R Basin*: QM W18280, Deep Ck, Bilyana; QM W14236, Murray R. Upper, below Murray Falls; QM W22150, Murray R. at Bruce Hwy crossing; *Hinchinbrook Island Basin*: QM W22013, Diamantina Ck, Hinchinbrook I.; QM W22014, South Zoe Ck, Hinchinbrook I.; QM W21929, Hinchinbrook I., 8th Creek; *Black R Basin*: QM W18282, Crystal Ck, below N.P.; NTM Cr006233, Crystal Ck; QM W22065, Black R. at Black R. road crossing; *Ross R Basin*: QM W21485, Alligator Ck below Bowling Green Bay N.P. near Townsville; *Water Park Ck Basin*: QM W19344, Sandy (=Cowan) Ck, road bridge, Shoalwater Bay area; QM W19335, Shoalwater Bay area, unnamed creek between Crab Camp and Sandy Ck; W19345, Shoalwater Bay area, creek at Freshwater Camp; QM W19328, The Three Rivers; *Fitzroy R Basin*: QM W7988, Moores Ck, Rockhampton; *Burrum R Basin*: QM W17972, Elliott R., Goodwood-Bundaberg Rd bridge; QM W17967, Gregory R., Childers-Goodwood Rd bridge; *Fraser Island Basin*: QM W2789, Lake McKenzie, Fraser I.; QM W4013, Cooneal Ck, Fraser I.; QM W16420, Fraser I.; *Noosa R Basin*: QM W17983, Big Tuan Ck near Tuan S.F. headquarters; QM W5084, Cooloola; QM W4545, Searys Ck, Cooloola; QM W5086, Freshwater Ck, Cooloola; QM W5091, Freshwater Lake, Cooloola; QM W5083, Kings Bore, Cooloola; QM W17173, Kin Kin Ck; QM W17163, Sunshine Ck, behind Sunshine Beach; *Pine R Basin*: QM W20004, Burpengary Ck at Oakey Flat road crossing; *Stradbroke – Moreton Islands Basin*: QM W209, Cowan Cowan, Moreton I.; QM W20605, Moreton I., creek c. 500 m south of Bulwer; QM W20604, Moreton I., creek c. 800 m south of Bulwer; W8292, Blue Lagoon, Moreton I.; QM W8020, North Stradbroke I. near Point Lookout; QM W15951, North Stradbroke I. near Adder Rock; QM W9726, Myora Springs, North Stradbroke I.; *Clarence R Basin*: AM P11186, Shelley Beach, Yaamba; AM P14439, Minnie Water near Grafton; *Bellingen R Basin*: QM W19934, Pinebrush Ck, Pacific Hwy crossing, Coffs Harbour; *Hawkesbury R Basin*: QM W21475, Nepean R. at Yarramundi Bridge, Richmond.

Diagnosis

Rostrum. Medium length in fully developed males, developmental range 0.48–0.9 CL (shortest in large females); moderately deep (maximum depth slightly more than dorsoventral diameter of eye); dorsal carina generally slightly sinuous, less commonly convex or straight, dentate along entire length, teeth subequally spaced, 9–11 teeth, 2–3 completely postorbital, number of teeth along proximal margin submoveable or all teeth immoveable in developed males; ventral carina dentate, 2–4 (-7) teeth, first tooth located in proximal half or at about mid-length.

General cephalon. Ocular cornea large, well-pigmented, accessory pigment spot present. Inferior orbit moderately produced, obtuse, post-antennular carapace margin evenly rounded. Bec ocellaire moderately developed. Scaphocerite elongated, length more than three times maximum breadth, lamina distinctly tapering from broadest point to anterior margin, anterior margin produced forward at inner angle. Epistome completely divided into two lobes, lobes rounded.

Mouthparts. Third maxilliped terminal segment clearly shorter than penultimate segment; exopod a little shorter than to about equal in length to ischiomerus. Mandibular molar process crowns as figured (Fig. 25D).

Second chelipeds (fully developed male). Larger and more developed than female P2; subequal in length, otherwise isomorphic; long, merus reaching distal end of scaphocerite; bearing simple and protective setae; all segments with closely-spaced, prostrate, squamiform protective setae; simple se-

tae few and scattered; fingers with well developed gape; pollex of moderate length, not noticeably broadened basally, about equal in breadth to basal dactylus, uncinate at tip, proximal cutting edge with dentate ridge or compound tooth followed by distinct gap, then large tooth, distally entire; dactylus of moderate length, uncinate at tip, proximal cutting edge with two or three closely spaced teeth, distinct gap, followed by third or fourth tooth on cutting edge, distally entire; manus subcylindrical, maximum breadth c. equal to maximum merus breadth, subcylindrical; carpus much shorter than chela, elongated, tapered; merus clearly shorter than carpus, elongated, tapered; ischium with well developed median groove on superior and inferior faces, tapered.

Third pereiopods (fully developed male). Long, propodus reaching distal end of scaphocerite; all segments covered with prostrate, squamiform protective setae; dactylus elongated, length about four times basal breadth, ventral carina well developed, most developed near base of unguis; unguis moderately developed, about one quarter length of remainder of dactylus.

Thoracic sternum. T4 with well-developed median process, postcoxal flanges situated posterior to and distinct from median process. Fully developed male T8 with anterolateral lobes contiguous posteromedially.

Abdomen. Inter-uropodal sclerite with strongly developed, elevated, pre-anal carina. Distolateral process on uropodal exopod with accessory spiniform seta mesially.

Body setation (fully developed male). Protective setation absent on carapace and abdomen.

Colour

Antennal and antennular flagella olive brown or orange brown to blue grey, inner antennular flagella darker, peduncles uniformly olive brown. Rostrum translucent blue grey with olive brown specks to uniformly deep olive brown on lateral and ventral carinae, translucent on dorsal carina. Ocular peduncles uniformly olive brown. Carapace mottled with olive brown blotches to uniform olive brown in fully developed males, abdomen olive grey speckled with olive brown to olive grey sometimes with a few cream blotches to uniform olive brown, tailfan deep blue grey with diaeresis on uropodal exopod marked with orange brown, ovigerous females with cream transverse band on tergite 3.

First chelipeds and ambulatory legs translucent olive grey with olive brown specks (particularly in young specimens) to uniformly olive grey to dark grey brown, joints orange brown, P1 finger tips light coloured. Second chelipeds with ischium of developed males characteristically orange brown, distal segments dirty olive brown to blue grey, indistinctly mottled with dark olive brown in females and young males, uniformly coloured in fully developed males, fingers dark brown with light coloured tips, tips generally white in young specimens, sometimes yellow or lime green to light brown, teeth on cutting edges of fingers blue grey.

Undeveloped eggs blue grey.

Life cycle

Euryhaline, adults collected from 0 to 17 ppt salinity but predominantly in fresh waters, eggs small and numerous, 819-5818 per brood (Kneipp, 1979), maximum length of developed ova 0.6 mm, larval development extended, requiring high salinity, c. 12 planktonic stages, minimum duration 38 days at 30 °C, 49 days at 25 °C, highest survival at 25–32 ppt salinity (Kneipp, 1979).

Size

Medium-sized species. Maximum size of developed male 32 mm CL, c. 120 mm TL. Maximum size of female 22 mm CL, 83 mm TL, minimum size of ovigerous female, 7 mm CL.

Habitat ecology

An adaptable species occurring in a wide range of perennial and seasonal water bodies on mainland and offshore sand islands – rivers, creeks, dune streams, marshes, springs, perched lakes, swamps, and water table seepage lagoons. The altitudinal distribution extends from near sea level to upper catchment headwaters, plateau streams and highlands (up to 800 m elevation). Substrates: fine to coarse, but mostly sand, gravel, rocks or bedrock.

Also found on humic sands in dune streams and lakes. Flow: zero to high (0–100 cm/sec recorded by Kneipp, 1979). Water clarity: low to high. Water depth: depths 0.1–2.0 m. Recorded physico-chemical tolerances: hardness < 10–80 ppm (field, $n = 21$), water temperature 17–34 °C (field, this study $n = 18$; Kneipp, 1979, $n > 100$), DO_2 1.8–9.9 ppm (field, $n = 13$), pH 5.0–8.0 (field, $n = 43$). Fringing vegetation: open communities dominated by *Eucalyptus*, *Melaleuca*, sedges, rushes, heathland to monsoon forest or rainforest, anthropogenically disturbed areas.

Behaviour

Sometimes active in daylight, particularly where fish predators are uncommon. Prefers to shelter in well-shaded areas underneath fallen timber, overhanging banks, boulders, rock ledges or in deep leaf litter beds.

Distribution

Eastern Drainage Region: Jacky Jacky Ck basin, Qld to Hawkesbury R. basin, N.S.W. Single isolated record from the Buckingham R. basin in the Northern Drainage Region.

Systematic position

Among Australian species, *M. tolmerum* appears closely allied to *M. auratum* sp. nov. The two species are so similar that they can only be reliably identified by the following combination of characters: (1) rostrum armed with 11 or more dorsal teeth and always failing to over-reach the distal end of the scaphocerite in *M. auratum* vs. rostrum often over-reaching the distal end of scaphocerite or if failing to do so with 10 or fewer dorsal teeth; (2) P2 of live developed male specimens of *M. tolmerum* with distinctive orange ischium vs. ischium of similar colour to more distal segments in *M. auratum*; (3) fingers of the minor P2 chela much shorter in length than the fingers of major P2 chela in developed males of *M. auratum* vs. fingers on major and minor P2 of similar length; (4) medium body size (up to 120 mm total body length) in *M. tolmerum* vs. small body size (up to 80 mm total body length) in *M. auratum*.

Vernacular names

East Australian river prawn.

Remarks

Although Riek (1951) reported the holotype to be a male, this appears to be an error. The specimen with holotype label in the Australian Museum collection closely matches Riek's original figure but is a non-ovigerous female. There is a large undeveloped male amongst the paratypes which does not match the size of 'adult male' provided by Riek and which is obviously not the specimen figured. The holotype is aberrant in having the fourth and fifth pleura posteroventrally acute. I have not observed this condition in any other individuals of the species.

The ovigerous female allotype designated by Riek is not *M. tolmerum* but instead *M. auratum* sp. nov. (this study). This was first noted by Kneipp (1979) in an unpublished Ph.D. thesis (as *Macrobrachium* sp. A).

The type locality given by Riek is also erroneous. Macrossan is situated on the Burdekin River (not the Black River) and is too far inland to fit Riek's description of the type locality, 'a purely freshwater habitat at least 5 miles above the tidal zone'. It is likely that Riek collected at the Black River probably somewhere near the railway line or old highway crossing, north of Townsville, about 80 km NNE of Macrossan. The Black River is sandy and ephemeral and normally flows for short periods during the wet season.

Although the holotype and paratypes do not include a fully developed male they are in reasonable condition and show most of the diagnostic characters of the species. Among the material examined are developed males from areas in the vicinity of the type locality. Numerous fully developed males have also been examined from a wide geographic range spanning nearly 3000 km along the east coast of Australia. The record from the Buckingham River Basin in the Northern Drainage Region is based on one ovigerous female and needs to be confirmed by examination of adult males from the area.

This is by far the most dominant and ubiquitous species in the Wet Tropics region of northeast Queensland. Interestingly, although its range extends southward to just north of Sydney, it is largely limited to offshore sand islands and coastal sand dune streams in subtropical Queensland and New South Wales. On some of the offshore sand islands it has shown remarkable dispersal capabilities by colonising isolated coastal lagoons immediately behind surf beaches.

An ingenious method for capturing this species was employed by aborigines of the Jirrbal language group in the upper Murray River area. A palm frond was stripped back to the mid-rib and the tip sharpened to create a lightweight spear. A quantity of human saliva (in low nutrient waters prawns are quickly attracted to small quantities of potential food, including saliva) was placed on the tip and the spear laid in the water. When a prawn picked up the tip with its pereiopods and moved it to its mouth to feed the base of the spear would be tapped forcefully using the palm of the hand, effectively spearing the prawn through its mouth. It is possible the same method was used by Jirrbal people in the upper Tully area to capture *M. koombooloomba* sp. nov.

Macrobrachium auratum sp. nov. (Figs 27, 28, 36C, 37A, B)

Macrobrachium tolmerum Riek, 1951, p. 362 (in part).

Material examined

Holotype. *Eastern Drainage Region. Proserpine R Basin*: QM W22092, 1 male, CL 19.6 mm, Flame Tree Ck between Airlie Beach and Shute Harbour, 20° 16' S, 148° 45' E, 2/6/1997, J. Short, A. Humpherys.

Paratypes. *Eastern Drainage Region. Endeavour R Basin*: QM W16907, 3 males, CL 6.2–15.6 mm, 3 females, CL 4.3–9.9 mm, 1 imm., CL 4.2 mm, Jensens Crossing, Endeavour R., 15° 26′ S, 145° 07′ E, 6/11/1990, J. Short, P. Davie; QM W22040, 3 males, CL 9.0–16.9 mm, 3 ovig. females CL 8.1–10.3 mm, 4 females CL 6.3–9.0 mm, Endeavour R. above first falls, 15° 25′ S, 145° 06′ E, 8/6/1997, J. Short, P. Graham; *Daintree R Basin*: QM W22078, 3 males, CL 7.4–11.0 mm, 1 ovig. female, CL 9.4 mm, Bloomfield R. below first falls, 15° 57′ S, 145° 18′ E, 16/6/1997, J. Short, P. Graham; *Mulgrave-Russell Rivers Basin*: QM W22206, 1 male, CL 14.9 mm, 1 ovig. female, CL 8.5 mm, Josephine Ck, crossing on road to Josephine Falls, 17° 25′ S, 145° 53′ E, 12/6/1997, J. Short; *Johnstone R Basin*: QM W18723, 2 ovig. females, CL 8.1, 11.5 mm, Tregothanaan Ck, 17° 31′ S, 145° 37′ E, QDPI (Fisheries), Johnstone R. survey; QM W19647, 2 males, CL 14.1, 17.7 mm, 3 ovig. females, CL 13.2–14.5 mm, Utchee Ck, 17° 37′ S, 145° 57′ E, 22/10/1991, QDPI (Fisheries), Johnstone R. survey; *Black R Basin*: QM W18283, 1 male, CL 13.1 mm, Crystal Ck, below N.P., 18° 58′ S, 146° 16′ E, 30/12/1992, J. Short; QM W18284, 2 males, CL 11.5, 14.9 mm, same locality data; AM P28177, 20 males, CL 9.3–14.6 mm, 2 females, CL 7.6, 11.9 mm, Bluewater Ck near Townsville, 19° 15′ S, 146° 29′ E, 1978, I. Kneipp; *Haughton R Basin*: QM W18263, 1 female, CL 14.2 mm, Reid R., bridge on Townsville-Charters Towers Rd, 19° 45′ S, 146° 50′ E, 22/12/1992, J. Short; *Burdekin R Basin*: AM P13298, 2 males, CL 11.0, 11.2 mm, 2 ovig. females, CL 12.7, 13.3 mm, 1 female, CL 10.2 mm, Burdekin R., 16 km SW of Ayr, 5/10/1950, E.F. Riek; *Don R Basin*: QM W22049, 1 male (16.0 mm CL), Elliott R., Guthulungra, 19° 55′ S, 147° 50′ E, 2/6/1997, J. Short, A. Humpherys; QM W22050, 1 female, CL 20.1 mm, same locality, 2/6/1997, J. Short, A. Humpherys; QM W22184, 2 ovig. females, CL 12.0, 15.7 mm, 1 female, CL 12.8 mm, same locality, 25/6/1997, J. Short; AM P13300, 1 male, CL 16.9 mm, Elliott R., between Bowen and Ayr, 19° 26′ S, 147° 51′ E, 1/10/1950, E.F. Riek; *O'Connell R Basin*: QM W22157, 3 males CL 7.3–9.6 mm, 7 females CL 7.9–16.1 mm, Murray Ck, Rostirollas Rd crossing near Mt Ossa, 20° 58′ S, 148° 48′ E, 25/6/1997, J. Short; *Plane Ck Basin*: QM W22223, 1 male CL 21.9 mm, Flaggy Rock Ck upstream of Bruce Hwy, 21° 58′ S, 149° 25′ E, 26/6/1997, J. Short; QM W22148, 2 males CL 5.7, 7.3 mm CL, Marion Ck, crossing upstream of Bruce Hwy near Ilbilbie, 21° 42′ S, 149° 21′ E, 26/6/1997, J. Short; QM W22190, 1 male CL 15.1 mm, 1 female, CL 12.2 mm, Sandy Ck, Homebush, 21° 16′ S, 149° 02′ E, 26/6/1997, J. Short.

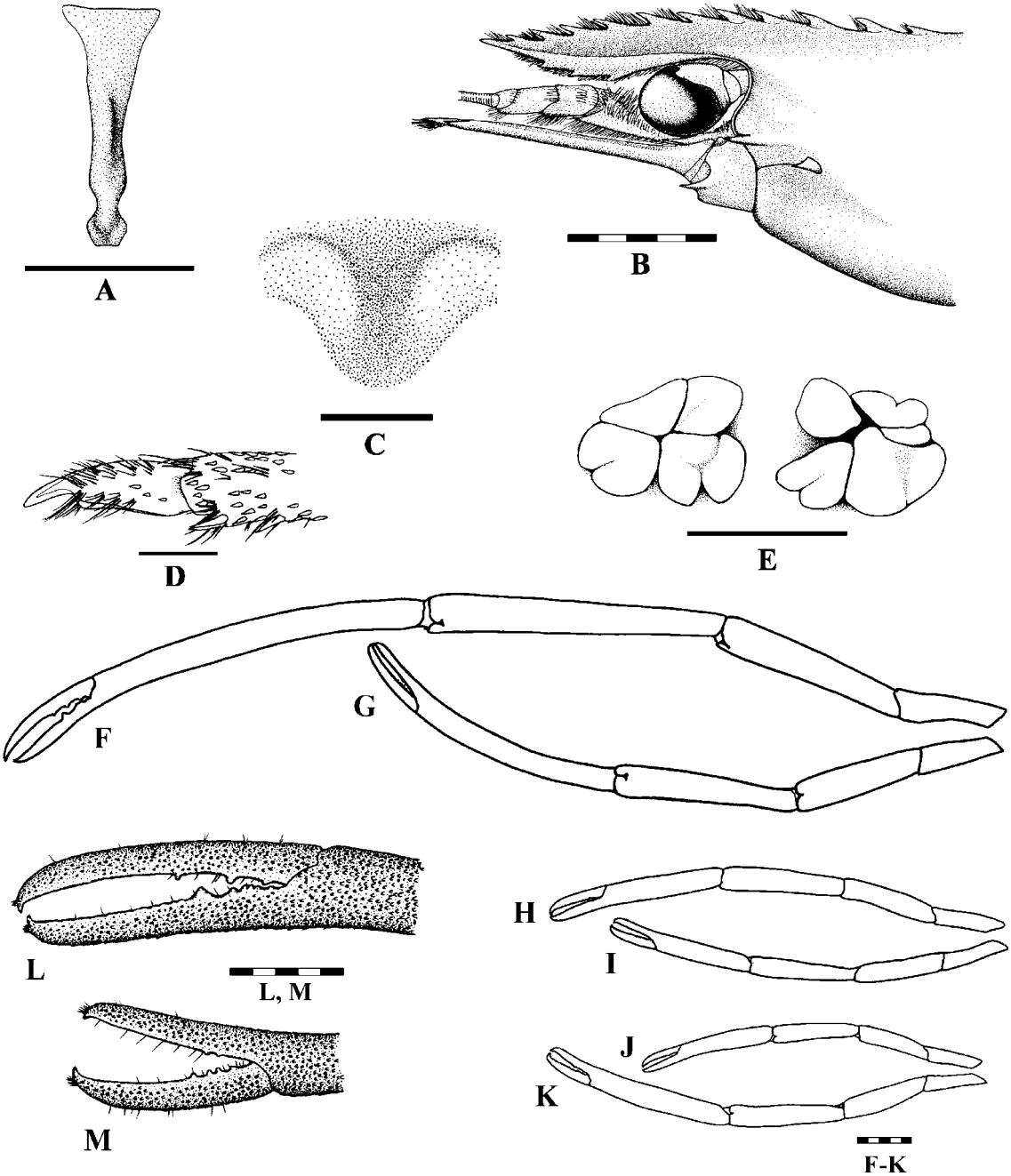

Figure 27. Macrobrachium auratum sp. nov. (A) QM W19647, paratype male 17.6 mm CL, ventral view of inter-uropodal sclerite, (B) QM W18283, paratype male 13.1 mm CL, anterior cephalothorax, (C) QM W16907, paratype male 15.6 mm CL, epistome, (D) QM W22092, holotype male 19.5 mm CL, dactylus and distal propodus of fully developed left third pereiopod, (E) QM W16907, paratype male 15.6 mm CL, crowns of left and right mandibular molar processes (setae omitted), (F) QM W22092, holotype male 19.5 mm CL, fully developed major second cheliped (protective setation omitted), (G) Fully developed minor second cheliped (protective setation omitted), (H) QM W22184, paratype ovig. female 15.7 mm CL, major second cheliped (protective setation omitted), (I) minor second cheliped (protective setation omitted), (J) QM W22040, paratype male 14.0 mm CL, undeveloped minor second cheliped (protective setation omitted), (K) undeveloped major second cheliped (protective setation omitted), (L) QM W22092, holotype male 19.5 mm CL, fingers and distal manus of fully developed major chela, (M) fingers of fully developed minor chela. Solid scale bars and divisions on divided scale bars 1 mm.

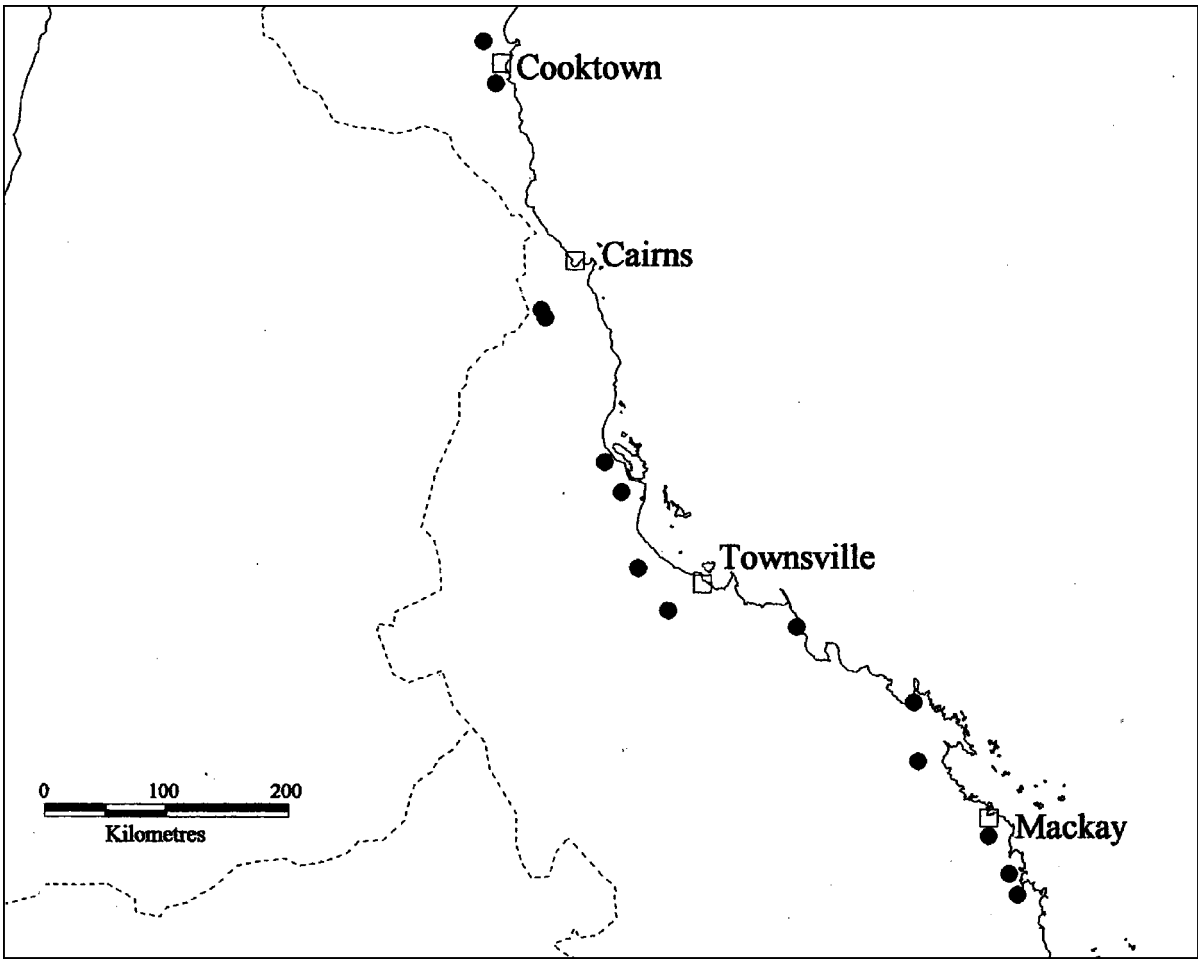

Figure 28. Distribution of *Macrobrachium auratum* sp. nov.

Allotype of *Macrobrachium tolmerum* Riek, 1951. *Eastern Drainage Region*. *Black R Basin*: AM P11989, 1 ovig. female, CL 14.6 mm, Black River, Macrossan (erroneous locality), E.F. Riek, October 1943.

Paratypes of *Macrobrachium tolmerum* Riek, 1951. AM P55010, 3 females, CL 14.2–15.2 mm, same locality as allotype (part of paratypic series).

Additional material. *Eastern Drainage Region*. *Endeavour R Basin*: QM W16896, 1 male, CL 14.9 mm, north branch Endeavour R., Battle Camp-Cooktown Rd crossing, 6/11/1990, J. Short, P. Davie; *Burdekin R Basin*: AM P13301, 4 males, CL 15.8–20.0 m, 3 ovig. females, CL 13.6–18.9 mm, 3 females, CL 11.2–15.9 mm, Burdekin R., 16 km south of Bowen, 26/9/1950, E.F. Riek.

Description

Rostrum. Rostrum short (of medium length in some of the smaller paratypes), 0.6 CL (0.45–0.89 in paratypes); moderately deep (maximum depth slightly more than dorsoventral diameter of eye); dorsal carina convex (slightly sinuous in some paratypes), dentate along entire length, teeth subequally spaced, 12 teeth (11–14 in paratypes), 3 completely postorbital (3–4, rarely 2 or 5 in paratypes), number of proximal teeth submoveable (moveable in smaller paratypes); ventral carina armed with 3 teeth (2–5 in paratypes), first tooth located slightly in proximal half (or at mid-length in some paratypes).

General cephalon. Ocular cornea large, well-pigmented, accessory pigment spot present.

Inferior orbit moderately produced, obtuse, postantennular carapace margin evenly rounded. Bec ocellaire moderately developed. Scaphocerite elongated, length c. 3 times maximum breadth, lamina distinctly tapering from broadest point to anterior margin, anterior margin produced forward at inner angle. Epistome completely divided into two lobes, lobes rounded, well separated.

Mouthparts. Third maxilliped terminal segment clearly shorter than penultimate segment; exopod clearly shorter than ischiomerus. Mandibular molar process crowns as figured (Fig. 27E).

Second chelipeds (developed males). Isomorphic in setation and shape, distinctly unequal in length; long, distal end of merus of minor cheliped just reaching distal end of scaphocerite; bearing simple and protective setae; all segments with closely-spaced, prostrate, squamiform protective setae; simple setae few and scattered except for few tufts on fingers; fingers with well developed gape; pollex elongated, uncinate at tip, not noticeably broadened basally, about equal in breadth to basal dactylus, proximal cutting edge of major chela pollex with small dentate ridge, followed by small but distinct gap then series of low medium-sized teeth (continuous ridge of small teeth in some developed male paratypes only one tooth in one developed male paratype), followed by distinct gap and large incisor tooth (sometimes two large well separated teeth in developed male paratypes with the distal tooth the larger), distally entire, proximal cutting edge of minor chela pollex with two small teeth (series of small teeth followed by gap then large tooth or series of four teeth in developed male paratypes); dactylus elongated, uncinate at tip, proximal cutting edge of major chela with three well developed teeth (sometimes four in developed male paratypes, two in one developed male paratype), the first opposing first ridge on pollex, the second slightly advanced of series of medium-size teeth on pollex, third tooth somewhat advanced of large tooth on pollex, distally entire, proximal cutting edge of minor chela dactylus with four well spaced proximal teeth (three in some developed male paratypes), distally entire; manus slightly compressed proximally, well compressed distally, mesially curved (straight in some developed male paratypes), over twice length of dactylus; carpus much shorter than chela, tapered; merus much shorter than carpus, tapered, slightly inflated subdistally; ischium with deep median groove on superior face, shallower groove on inferior face (major cheliped only, absent on both chelipeds of some developed male paratypes), moderately short, compressed, tapered.

Third pereiopods. Short, dactylus reaching distal end of scaphocerite; covered with prostrate, squamiform protective setae; dactylus stout, length c. three times basal breadth, ventral carina well developed; unguis strongly developed, slightly less than half length of remainder of dactylus.

Thoracic sternum. T4 with well-developed median process, postcoxal flanges situated posterior to and distinct from median process. Male T8 with anterolateral lobes contiguous posteromedially, without distinct median process posteriorly (spinate median process present in one developed male and several small undeveloped male paratypes).

Abdomen. Inter-uropodal sclerite with strongly elevated pre-anal carina. Distolateral process on uropodal exopod with accessory spiniform seta mesially.

Body setation. Protective setation absent on carapace and abdomen.

Colour

General body colour light cream or gold (light substrate habitats) to bronze or dark rusty brown (dark substrate habitats). The following description is based on specimens from Crystal Creek.

Antennae translucent, tinged with gold, scaphocerites similar but with a few gold blotches. Rostrum translucent, tinged with olive yellow to gold. Ocular peduncles translucent, tinged with gold. Body golden cream indistinctly specked with gold or olive yellow to mottled with dark brown blotches, abdomen sometimes with lighter cream blotches on tergites, telson and uropods translucent gold, sometimes also with light cream blotches.

Ambulatory legs translucent with faint gold or cream blotches to indistinctly banded with alternating bronze and olive brown transverse blotches. Second chelipeds olive yellow ornamented with striking dark grey blotches, blotches often tending to ring segments but sometimes more irregular or joining together to form longitudinal bands in large specimens, transverse banding very conspicuous on fingers and distal manus.

Life cycle

Euryhaline, adults occurring in 0–17 ppt salinity (Kneipp, 1979), predominantly in fresh waters, eggs small and numerous, c. 500–6000 per brood, maximum length of developed ova 0.6 mm. Larval cycle unstudied but egg size indicative of lengthy development.

Size

Small species. Maximum size of developed male 22 mm CL, 80 mm TL. Maximum size of female similar to male, minimum size of ovigerous female, 8 mm CL.

Habitat ecology

Perennial and seasonal rivers and creeks from lowlands to foothills (to 80 m elevation). Substrates: sand, gravel or rocks. Flow: zero to high (0–100 cm/s recorded by Kneipp, 1979). Water clarity: fair to high. Water depth: mostly collected from depths between 0.1 and 0.5 m during this study. Kneipp (1979) also indicated a preference for depths around 0.3 m. Recorded physicochemical tolerances: water temperature 17.7–36.5 °C (field, this study $n = 11$; $n > 50$, Kneipp, 1979), hardness < 10–180 ppm (field, $n = 11$), DO_2 4.6–9.6 ppm (field, $n = 11$), pH 6.0–8.0 (field, $n = 12$). Fringing vegetation: open communities dominated by *Eucalyptus*, *Casuarina* or *Melaleuca* to rainforest.

Behaviour

Reasonably active in daylight, common in unshaded mid-stream areas and along unshaded banks. Prefers to shelter underneath rocks in shallow running water where it is often collected with the atyid shrimp, *Australatya striolata*.

Etymology

Derived from the latin, '*auratus*' (ornamented with gold), and referring to the typical body colour of the species when collected from habitats with light coloured substrates.

Distribution

Eastern Qld: Endeavour R. basin to Plane Ck basin.

Systematic position

The new species appears closely allied to the South Pacific species, *M. aemulum* (Nobili, 1906). It differs in having a well-developed median process on thoracic sternite 4 (poorly developed in *M. aemulum*). The fingers of the major P2 are also relatively shorter and clearly less than half the length of the manus (one third of the length of the manus in fully developed males) whereas in *M. aemulum* the fingers are much longer than half the manus.

The new species is also closely allied to *M. tolmerum*. The differences between the two taxa are discussed above under *M. tolmerum*.

Vernacular names

Golden river prawn.

Remarks

The new species was first recorded from Bluewater Ck near Townsville by Kneipp (1979) in an unpublished Ph.D. thesis (as *Macrobrachium* sp. A). As noted by Kneipp, the ovigerous female allotype and part of the paratypic series of *M. tolmerum* Riek belong instead to this species. The above description is based on 75 specimens collected from Cooktown, NE. Qld to Flaggy Rock Ck between Sarina and Rockhampton, ME.Qld.

The new species shows a distinct preference for running water and is most easily collected under rocks in shallow riffle areas. Compared to *M. tolmerum* it is also more active in well-lit areas during daylight. At some localities, such as Crystal Creek, this is a highly attractive species and individuals are often beautifully flecked with gold and cream.

Macrobrachium lar (Fabricius, 1798) (Figs 29, 30, 36K)

Restricted synonymy
Palaemon Lar Fabricius, 1798, p. 402.

Macrobrachium lar – Maki & Tsuchiya, 1923, p. 56, pl. 5, fig. 1. Holthuis, 1950, pp. 16, 108 (key), 176–190 (complete earlier literature). 1955, fig. 34b. 1980, pp. 96–97. Riek, 1951, p. 362, fig. 2a, b. Maccagno & Cucchiari, 1957, pp. 281 (key), 333–336 fig. 37. Atkinson, 1977, pp. 119–132, figs 1–6. Liu et al., 1990, pp. 104, 123–124, fig. 21. Shy & Yu, 1998, pp. 34–35. Short & Marquet, 1998, p. 403 (key). Keith et al., 1999, pp. 54–55. Yeo et al., 1999, pp. 236. Short & Meek, 2000, pp. 82–83. Short, 2000, p. 64. Cai & Ng, 2001, p. 683. Wowor & Choy, 2001, p. 285.

Not *Palaemon ornatus* – Baker, 1914, p. 447 (=*M. australiense* Holthuis, 1950).

Material examined

Northern Drainage Region. *Roper R Basin*: QM W24028, Roper R.; *Eastern Drainage Region*. *Jeannie R Basin*: QM W20598, Cape Melville Ra., west side, water point; QM W22029, McIvor R., Isabella-McIvor Rd crossing; *Endeavour R Basin*: QM W22020, Annan R. near Shiptons Flat; QM W22036, Endeavour R. just above first fall; QM W22024, Trevethan Ck, Cooktown Developmental Rd crossing; *Barron R Basin*: QM W16638, Stony Ck, Kamerunga; *Mulgrave-Russell Rivers Basin*: QM W8022, Wright Ck, south of Cairns; QM W16288, Little Mulgrave R., Orchid Valley; QM W14576, Mulgrave R., south of Cairns; *Johnstone R Basin*: QM W19665, Fisher Ck; QM W21490, Fischer Ck at Fischer Ck Rd bridge; QM W19640, Mena Ck; QM W22181, The Coconuts, Flying Fish Pt Rd, small unnamed creek; QM W22005, The Coconuts, on Flying Fish Pt Rd, small unnamed creek; *Herbert R Basin*: QM W19660, Palm I.

Diagnosis

Rostrum. Short in fully developed males, developmental range 0.5–0.7 CL; moderately deep (maximum depth slightly more than dorsoventral diameter of eye); dorsal carina sinuous or upturned, dentate along entire length, teeth tending to be more closely spaced at mid-length, 7–10 teeth, 1–2 completely postorbital, all teeth immoveable in developed males; ventral carina dentate, 2–4 teeth, first tooth located in proximal half or at about mid-length of ventral carina.

General cephalon. Ocular cornea large, well-pigmented, accessory pigment spot present. Inferior orbit moderately produced, obtuse, post-antennular carapace margin evenly rounded. Bec ocellaire moderately developed. Scaphocerite stout, length slightly less than three times maximum breadth, lamina distinctly tapering from broadest point to anterior margin, anterior margin produced forward at inner angle or evenly rounded (large adults). Epistome completely divided into two lobes, lobes strongly produced antero-ventrally.

Mouthparts. Third maxilliped terminal segment clearly shorter than penultimate segment; exopod slightly shorter than ischiomerus to about equal in length. Mandibular molar process crowns as figured (Fig. 29E).

Second chelipeds. Isomorphic in setation and shape, unequal in length; long, merus of minor cheliped reaching distal end of scaphocerite; bearing simple and protective setae; protective setae abundant on all segments, well spaced and mamilliform on pollex, closely spaced and squamiform on lateral dactylus, widely spaced and mamilliform on mesial dactylus, closely spaced and squamiform on manus (interspersed with slightly flattened mamilliform protective setae), squamiform on carpus, merus and ischium, more erect on proximomesial merus and mesial ischium, those on proximomesial merus slightly elevated; simple setae few and scattered; fingers with well developed gape; pollex elongated, not noticeably broadened basally, about equal in breadth to basal dactylus, strongly uncinate at tip, proximal cutting edge with dentate ridge ending in tooth, distinct gap then very large incisor tooth, distally entire; dactylus elongated, arched, strongly uncinate at tip, proximal cutting edge with few low crenulations then very large incisor tooth well advanced of most distal tooth on pollex, distally entire; manus nearly cylindrical, maximum breadth clearly greater than maximum merus breadth, much longer than dactylus; carpus of moderate length, less than half length of chela, tapered; merus slightly longer than carpus, narrowed at mid-length; ischium moderately short, with well developed median groove on both superior and inferior faces, compressed, narrowed at mid-length.

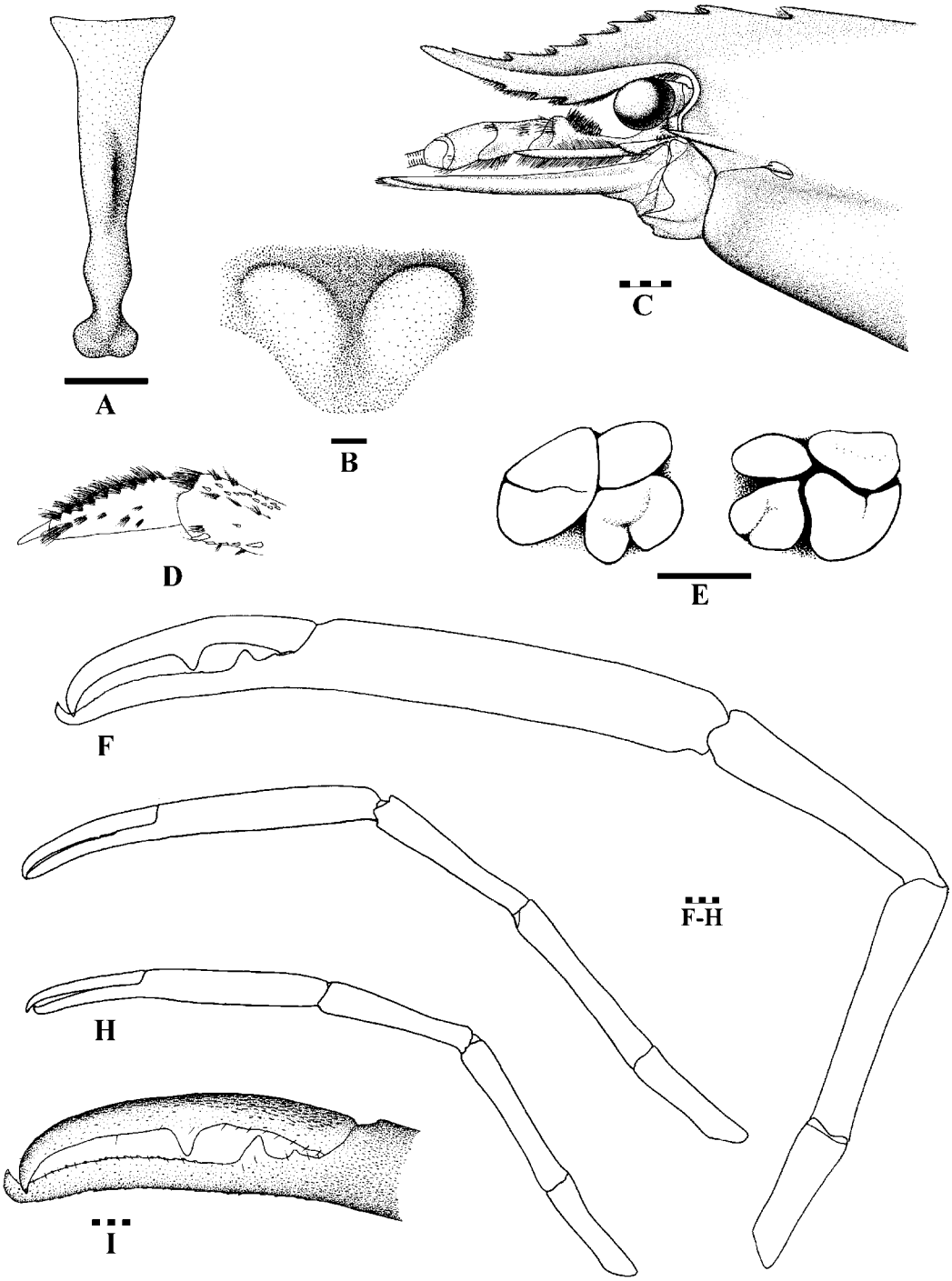

Figure 29. *Macrobrachium lar* (Fabricius, 1798). (A) QM W19640, male 43.8 mm CL, ventral view of inter-uropodal sclerite, (B) QM W14576, male 61.0 mm CL, epistome, (C) anterior cephalothorax of same, (D) QM W22020, male 58.0 mm CL, dactylus and distal propodus of right third pereiopod, (E) QM W14576, male 61.0 mm CL, crowns of left and right mandibular molar processes (setae omitted), (F) fully developed right second cheliped (protective setation omitted), (G) QM W22024, male 45.0 mm CL, undeveloped right second cheliped (protective setation omitted), (H) QM W22005, ovigerous female 43.8 mm CL, right second cheliped (protective setation omitted), (I) QM W14576, male 61.0 mm CL, fingers and distal manus of fully developed right cheliped. Solid scale bars and divisions on divided scale bars 1 mm.

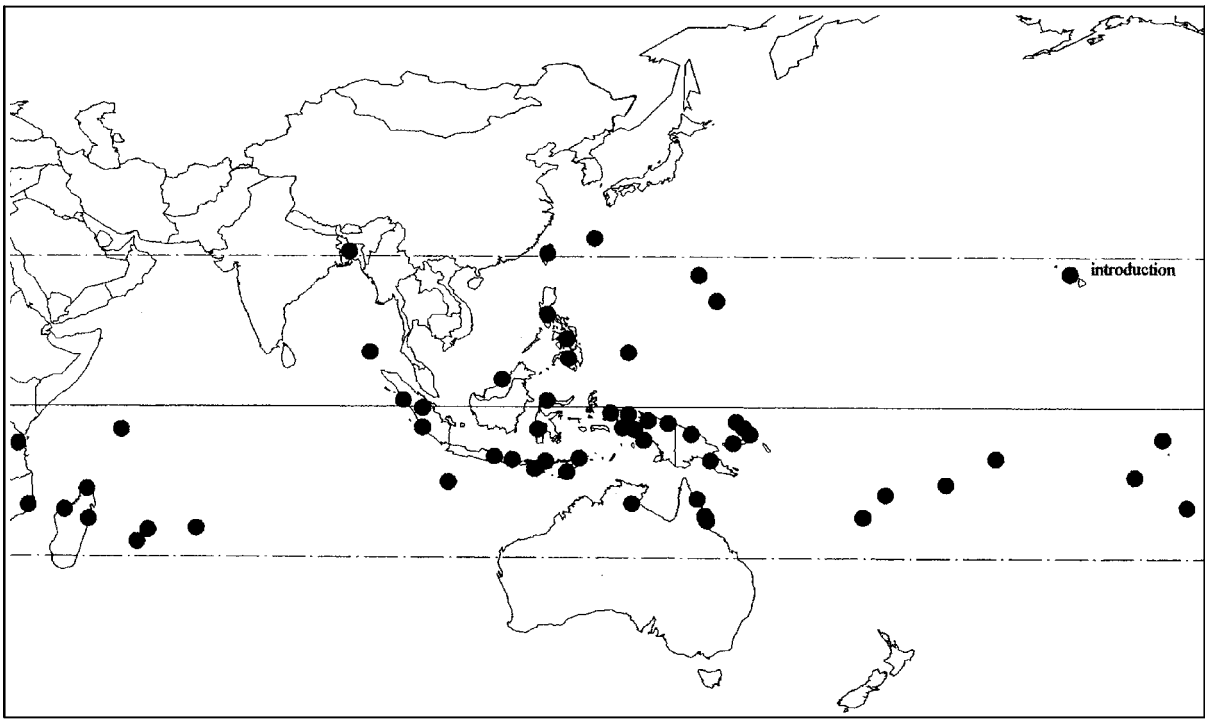

Figure 30. Distribution of *Macrobrachium lar* (Fabricius, 1798).

Third pereiopods (fully developed male). Long, propodus reaching distal end of scaphocerite; squamiform protective setae abundant on all segments except dactylus; dactylus stout, length slightly more than three times basal breadth, ventral carina moderately developed; unguis moderately developed, one-third to one-fifth length of remainder of dactylus.

Thoracic sternum. T4 with well-developed median process, postcoxal flanges situated posterior to and distinct from median process. Developed male T8 with anterolateral lobes well developed, contiguous posteromedially, without distinct median process posteriorly (blunt process present in young males).

Abdomen. Inter-uropodal sclerite with strongly developed pre-anal carina. Distolateral process on uropodal exopod with accessory spiniform seta mesially.

Colour

Antennal flagella deep olive grey to olive brown or orange, antennular flagella orange brown to almost black, scaphocerites translucent orange brown or olive grey to almost black or blue grey, peduncles olive brown to almost black. Rostrum olive grey to olive brown with dorsal teeth and plumose setae orange brown. Ocular peduncles deep orange brown. Body colour deep olive brown to olive grey or blue grey without specks or blotches, often somewhat variegated with swirls of orange brown, blue grey and light olive grey, abdominal condyles light cream to orange, posterior abdomen often darker than anterior and tergum darker than pleura.

First chelipeds and ambulatory legs blue grey to dark brown. Second chelipeds olive to dark brown, sometimes marbled with irregular brown, olive or blue-grey blotches, fingers dark reddish brown with pink mark on manus at base of dactylus.

Life cycle

Adults predominantly in fresh waters juveniles reported from estuaries, lowland fresh waters and

inshore marine areas; eggs small and very numerous, up to 40 000 per brood (Kubota, 1972), maximum length of developed ova 0.9 mm; larval development extended, at least 11 planktonic stages, over 89 days to metamorphosis in seawater at 23–26.5 °C (Atkinson, 1977).

Size

Large species. Maximum recorded size of developed male 61 mm CL, 195 mm TL (this study). Maximum size of female 44 mm CL, c. 145 mm TL (this study), minimum size of ovigerous female, 14 mm CL.

Habitat ecology

Largely restricted to permanently-flowing rivers and creeks from lowlands (near sea level) to foothills (to 150 m elevation in this study). Also occurs on offshore continental islands. On small oceanic islands in the Indo-West Pacific this species often extends further upstream to upland headwaters. Substrates: fine to coarse, silt and sand to bedrock. Flow: low to high, generally in pools near riffles in areas of moderate flow. Water clarity: generally high. Water depth: collected from depths ranging from 0.3 to 1.5 m. Two juvenile specimens recorded by Holthuis (1950) from a depth of 55 m (Siboga Stn 47, Bay of Bima, Sumbawa, reef, bottom mud with patches of fine coral sand). Recorded physicochemical tolerances: water temperature 20.7–28.2 °C (field, $n = 5$), DO_2 6.1–9.0 ppm (field, $n = 6$), pH 6.0–7.1 (field, $n = 6$), hardness < 20–40 ppm (field, $n = 2$). Fringing vegetation: anthropogenically disturbed to pristine rainforest, monsoon forest or open riparian.

Behaviour

Prefers to shelter in dark places under extensive cover such as piles of fallen timber or large boulders during the day, generally near flowing water. At night very shy of light and quickly moves away from the beam of a torch light.

Distribution

Wide-ranging Indo-West Pacific: eastern Africa to the Ryukyu Islands and Marquesas [type locality: East Indies]. Introduced to the Hawaiian Islands (Atkinson, 1977). *Australian distribution:* Jeannie R. basin to the Herbert R. basin, Eastern Drainage Region; Roper R. basin, Northern Drainage Region.

Systematic position

Among Indo-West Pacific species, fully developed males of *M. lar* are highly distinctive and are easily distinguished by the short, sinuous rostrum and long, robust second pereiopods with widely gaping fingers each bearing a large incisor tooth on the cutting edge. The species is most easily confused with *M. tolmerum*, *M. aemulum* and *M. auratum* sp. nov. but differs in the following characters:

1. P2 merus clearly longer than carpus in *M. lar* vs. clearly shorter than the carpus.
2. P2 fingers long and greater than half the length of manus in developed males in *M. lar* vs. clearly less than half the length of the manus.
3. Epistome lobes strongly produced anteroventrally in adults in *M. lar* vs. epistome lobes rounded.

Vernacular names

Giant jungle prawn, Monkey river prawn (FAO); Oura-pape (Tahiti: French Oceania), Paeho – females, Hetou – juveniles, Tipu (Nukuhiva, Marquesas), Akae (Fatuhiva, Marquesas), Hakae (Uapou, Marquesas) (cf. Holthuis, 1980).

Remarks

This is by far the most widespread species of the genus and has been well described by many authors e.g. De Man (1892), Cowles (1914), Holthuis (1950). Australian material agrees closely with previous descriptions.

Palaemon ornatus Olivier, 1811 is in all probability a junior synonym of this species. Baker's record from Hermannsburg, N.T. is more likely *M. australiense*, the only species occurring in endorheic streams in inland Australia.

The questionable record from Sydney (collected by R. Schütte) reported by Holthuis (1950)

is erroneous. The species has a strictly tropical distribution in northeast Australia. It is likely that the specimen was wrongly labelled, like much of Schütte's material.

In Australia, *M. lar* is most common in the Wet Tropics region of North-east Queensland, although it is not easily collected anywhere due to its secretive behaviour. It shows a preference for well-oxygenated water and is usually found near riffles or water falls, particularly where there is abundant shelter, such as large rocks, fallen timber or large tree roots.

The two giant river prawns, *M. lar* and *M. rosenbergii* are mostly allopatric in Australia, although they occur together in the McIvor River, NE. Qld. *M. rosenbergii* occurs across the seasonally wet or 'monsoonal' north, mostly in long, slow flowing rivers, whereas *M. lar* is most abundant in the Wet Tropics of North-east Queensland in high gradient, rainforest streams. The McIvor River is near the border of these two climatic zones. In the McIvor River, *M. lar* shows a preference for running water in rocky areas whereas *M. rosenbergii* is found in backwaters with fallen timber.

Riek (1951) recorded *M. lar* from the Roper River in the Northern Territory without giving a precise locality. No further material of the species was recorded from the Northern Territory during this study.

Macrobrachium latidactylus (Thallwitz, 1891) (Figs 31, 32)

Restricted synonymy

Palaemon latidactylus Thallwitz, 1891, p. 97. 1892, p. 17, pl. 1, fig. 3. Cowles, 1914, p. 392, pl. 3, fig. 10.

Macrobrachium latidactylus: Holthuis, 1950, pp. 16, 111 (key), 239–244, fig. 50a–h (complete earlier literature). 1980, p. 97. Maccagno & Cucchiari, 1957, pp. 281 (key), 336–339, fig. 38. Johnson, 1963, p. 16. Leggett, 1983, p. 65. Bruce, 1992, fig. 5A–C. Liu et al., 1990, pp. 103 (key), 112–113, fig. 10. Shy & Yu, 1998, p. 36–37. Yeo et al., 1999, p. 236. Cai & Ng, 2001, p. 682, fig. 15.

Material examined

Eastern Drainage Region. Lockhardt R Basin: QM W7256, Line Hill, Iron Ra.; *Stewart R Basin*: AM P13294, Massey R. (=Massy Ck?); QM W21562, Rocky R., Silver Plains Stn; *Endeavour R Basin*: QM W16899, north branch Endeavour R., Battle Camp-Cooktown Rd crossing; QM W5429, Endeavour R., 19 km NW of Cooktown; QM W16906, Endeavour R., Jensens Crossing; QM W5430, Endeavour R., Airport Crossing near Cooktown; *Daintree R Basin*: QM W21518, Daintree R.; *Mossman R Basin*: AM P14437, Spring Ck, c. 3 km from Mowbray R.; QM W21896, Moores Gully, Trinity Beach; *Barron R Basin*: QM W19236, Barron R., Kamerunga Bridge; QM W14899, Barron R. near Cairns; *Mulgrave-Russell Rivers Basin*: QM W17253, Wright and Stony Ck junction, Page Rd, Edmonton; QM W8027, Wright Ck, south of Cairns; *Johnstone R Basin*: QM W22238, Ella Bay, small creek c. 1.4 km north of Heath Park; QM W19619, North Johnstone R.; QM W11972, Innisfail; QM W22000, Johnstone R. at hospital bridge, Innisfail; QM W21996, North Johnstone R. at Bruce Hwy bridge; *Murray R Basin*: QM W14240, Murray R., Tates Landing; *Hinchinbrook Island Basin*: QM W8008, Hinchinbrook I., north end; *Black R Basin*: NTM Cr006234, Crystal Ck; QM W22066, Black R. at Black R. Rd crossing.

Diagnosis

Rostrum. Short in fully developed males, developmental range 0.5–1.0 CL (this study), moderately deep (maximum depth slightly more than dorsoventral diameter of eye); dorsal carina convex or straight, dentate along entire length, teeth subequally spaced, 12–17 teeth, 3–5 completely postorbital, number of proximal teeth moveable in developed males (sometimes submoveable in fully developed males); ventral rostrum dentate, 2–5 teeth, first tooth located in proximal half or at about mid-length of ventral carina.

General cephalon. Ocular cornea large, well-pigmented, accessory pigment spot present. Inferior orbit feebly produced, angular, appearing truncated, postantennular carapace margin generally straight (sometimes slightly concave or convex).

Scaphocerite elongated, length 3 or more times maximum breadth, lamina distinctly tapering from broadest point to anterior margin, anterior margin

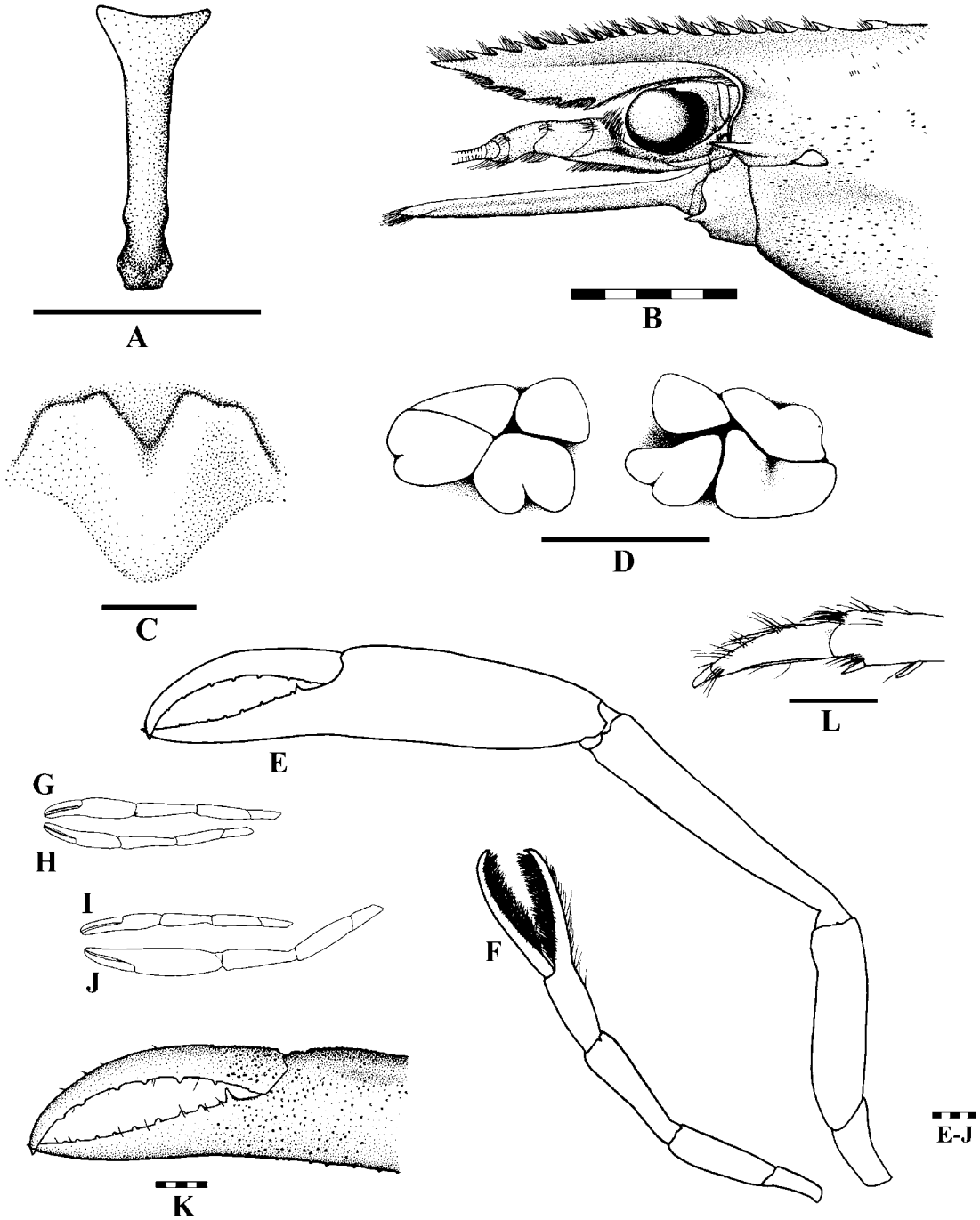

Figure 31. Macrobrachium latidactylus (Thallwitz, 1891). (A) QM W5430, male 13.5 mm CL, ventral view of inter-uropodal sclerite. (B) QM W11972, male 14.2 mm CL, anterior cephalothorax. (C) QM W7256, male 23.7 mm CL, epistome. (D) crowns of left and right mandibular molar processes (setae omitted). (E) fully developed major second cheliped (protective setation omitted). (F) fully developed minor second cheliped (protective setation omitted). (G) QM W19641, female 10.1 mm CL, right second cheliped (protective setation omitted). (H) left second cheliped (protective setation omitted). (I) QM W14899, male 11.2 mm CL, undeveloped minor second cheliped (protective setation omitted). J, undeveloped major second cheliped (protective setation omitted). (K) QM W7256, male 23.7 mm CL, fingers and distal manus of fully developed right cheliped. (L) QM W19619, male 15.6 mm CL, dactylus and distal propodus of right third pereiopod. Solid scale bars and divisions on divided scale bars 1 mm.

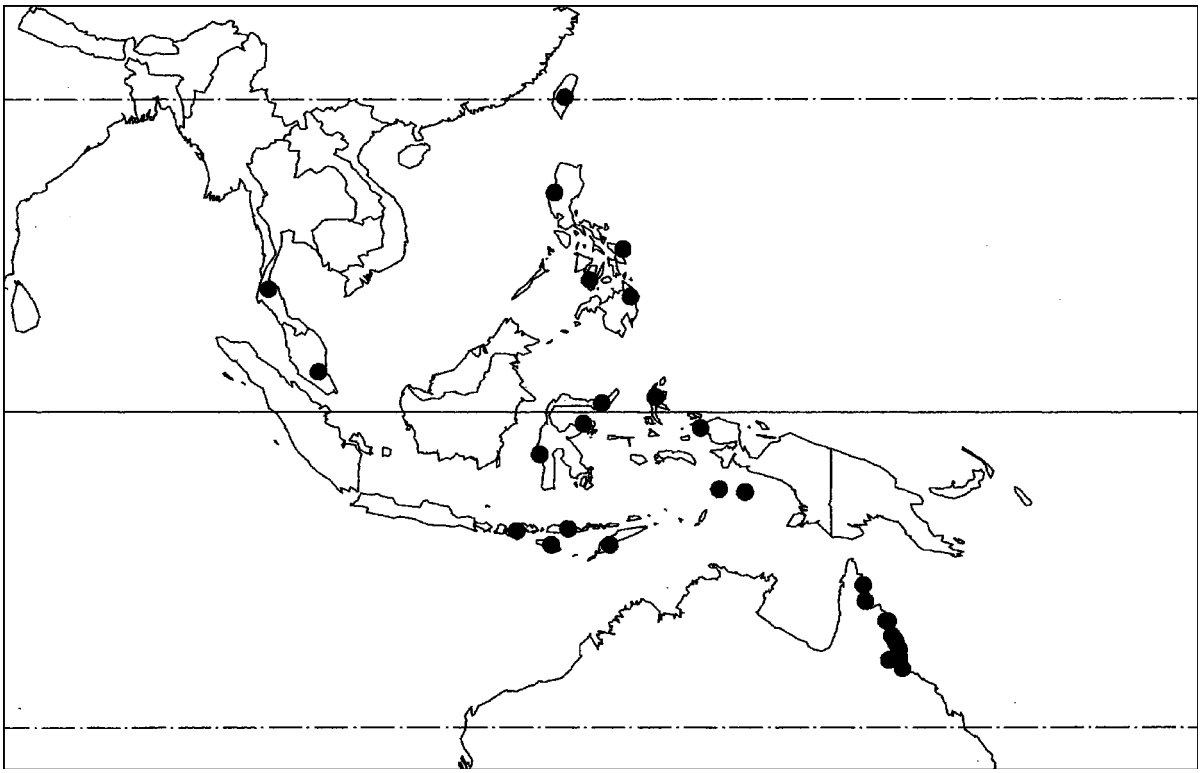

Figure 32. Distribution of *Macrobrachium latidactylus* (Thallwitz, 1891).

produced forward at inner angle. Epistome completely divided into two lobes, lobes moderately produced anteromesially.

Mouthparts. Third maxilliped terminal segment clearly shorter than penultimate segment; exopod about equal in length to ischiomerus. Mandibular molar process crowns as figured (Fig. 31D).

Second chelipeds (fully developed male). Larger and more developed than female P2; fully dimorphic; short, carpus of minor cheliped reaching distal end of scaphocerite; major cheliped bearing simple, multidenticulate and protective setae; all segments except distal fingers and lateral merus with erect mamilliform protective setae, most abundant on lateral manus, mesial merus and ischium; multidenticulate setae present on inferior manus, carpus and merus; fingers with well developed gape; pollex markedly tapered with broad base, deflected mesially at two-thirds length, broad basally, much broader than basal dactylus, cutting edge with large incisor tooth proximally followed by well-developed equally-spaced rounded teeth along length, teeth diminishing in size distally; dactylus strongly arched, cutting edge with three or four crenulations proximally followed by well developed, rounded, equally spaced teeth along length, teeth diminishing in size distally; manus elongated, compressed, broad, maximum breadth much greater than maximum merus breadth, much longer than dactylus; carpus much shorter than chela, elongated, tapered; merus much shorter than carpus, cylindrical, sometimes inflated in middle third, often noticeably narrowed subdistally; ischium very short, compressed, tapered, with well developed median groove on superior face, indistinct groove on inferior face.

Minor cheliped differing from major in having mamilliform protective setae on manus, merus, carpus and ischium less abundant than on major cheliped; with few simple setae on lateral merus and proximolateral carpus; multidenticulate setae forming well-developed, inwardly-directed brushes on cutting edges of fingers; cutting edge of pollex with small tooth proximally followed by well

developed median carina, dactylus similar except for series of crenulations proximal to tooth; pollex elongated, not noticeably broadened basally, about equal in breadth to basal dactylus; dactylus elongated, slender; manus compressed, maximum breadth less than or c. equal to maximum merus breadth, much shorter than dactylus; carpus tapered, slightly inflated distally; merus subcylindrical, inflated.

Third pereiopods (fully developed male). Short, dactylus just reaching distal end of scaphocerite; small mamilliform protective setae present on inferior merus only; dactylus stout, length c. three times basal breadth, ventral carina poorly developed; unguis moderately developed, one quarter to one third length of remainder of dactylus.

Thoracic sternum. T4 with well-developed median process, postcoxal flanges situated posterior to and distinct from median process. Fully developed male T8 with anterolateral lobes contiguous posteromedially, without median process posteriorly (spinate median process present in young males).

Abdomen. Inter-uropodal sclerite without preanal carina. Distolateral process on uropodal exopod with accessory spiniform seta mesially.

Body setation (fully developed male). Spinuliform protective setae on anterior carapace only, abundant anterolaterally; few scattered simple setae dorsally.

Colour (freshwater material)

Antennal and antennular flagella olive yellow, scaphocerites translucent specked with brown, peduncles olive yellow specked with rusty brown. Ocular peduncles specked with rusty brown. Rostrum translucent, specked with rusty brown. Body light olive grey with rusty brown specks arranged as few irregular blotches on lateral carapace, abdominal condyles marked with olive brown, transverse brown bands across tergites, third tergite with light transverse band, specks on telson and uropods red brown, distolateral processes on uropodal exopods marked with deep brown.

First chelipeds and ambulatory legs translucent, specked with rusty brown, joints light orange. Major second cheliped manus with longitudinal brown stripes on superior face, inferior face pale, dactylus banded on distal half, pollex dark brown, carpus and merus with irregular brown blotches. Minor second cheliped with pollex dark brown, faint longitudinal stripes on manus.

Life cycle

Euryhaline, 0–33 ppt salinity, amphidromous, adults most common in fresh water at the upstream limit of tidal influence, eggs small and numerous, 503–1605 per brood (Kneipp, 1979), maximum length of developed ova 0.6 mm, larval development extended, requiring brackish water, at least eight planktonic stages, minimum 21 days at 30 °C and 36 days at 25 °C, highest survival at 20–25 ppt salinity (Kneipp, 1979).

Size

Small species. Maximum size of developed male, 24 mm CL (this study), 80 mm TL (Holthuis, 1980). Maximum size of female 12 mm CL, 37 mm TL (this study), minimum size of ovigerous female, 9 mm CL (this study).

Habitat ecology

Prefers permanently-flowing rivers and creeks in coastal lowland areas from <5 to 40 m elevation. Also found on offshore continental islands. Substrates: fine to coarse. Flow: 0–60 cm/s with a preference for low flow conditions recorded by Kneipp (1979). Water clarity: low to high. Water depth: 0.1–1.5 m with a slight preference for shallower depths. Recorded physico-chemical tolerances: water temperature 21–37 °C (field, this study $n = 4$; Kneipp, 1979, $n > 100$), DO_2 9.6–11.5 ppm (field, $n = 3$), hardness < 20 ppm (field, $n = 5$), pH 6.2–8.0 (field, $n = 5$). Fringing vegetation: rainforest, mangroves.

Behaviour

Shelters underneath fallen timber, tree roots, and amongst leaf litter.

Distribution

Central Indo-West Pacific: Malaysia, Indonesia, the Philippines [type locality: North Celebes],

southern China. *Australian distribution:* North-east Qld: Olive-Pascoe Rivers basin to Black R. basin.

Systematic position

M. latidactylus is a highly distinctive species allied to *M. handschini* (Roux, 1933). It is easily distinguished from *M. handschini* and other Indo-West Pacific taxa by the morphology of the inferior orbit. In *M. latidactylus* the inferior orbit is feebly produced and appears truncated. The postantennular carapace margin is generally straight. In *M. handschini* the inferior orbit is moderately produced (as is typical of the genus) and rounded with the postantennular carapace margin convex. The two species can also be separated on the relative length of segments of both major and minor second pereiopods in adult males and females; in *M. latidactylus* the carpus is invariably longer than the merus whereas in *M. handschini* it is always shorter. The two species also have markedly different life cycles. The land-locked freshwater species, *M. handschini*, has moderately large ova (1.5 mm maximum length) whereas the euryhaline *M. latidactylus* has small developed ova (0.6 mm).

Vernacular names

Broad-fingered river prawn, Scissor river prawn (FAO).

Remarks

M. latidactylus has been well described by De Man (1892), Cowles (1914) and Holthuis (1950). Australian material examined in this study agrees well with previous descriptions. As described by Holthuis (1950), *M. latidactylus* shows high variability in the form of the second pereiopods of developed males.

Although this species is commonly encountered in the freshwater tidal zone of rivers in northeast Queensland it was not included in Riek's account of Australian freshwater species. *M. latidactylus* is a wide-ranging Central Indo-West Pacific species but is Australia appears limited to north-east Queensland.

The first Australian record was in a checklist of freshwater fishes and Crustacea from Hinchinbrook I., NE.Qld, by Leggett (1983) and was based on material identified at the Queensland Museum.

Macrobrachium handschini (Roux, 1933) (Figs 33–35, 36H, I)

Palaemon (Macrobrachium) handschini Roux, 1933, pp. 345–346.
Macrobrachium glypticum Riek, 1951, pp. 360 (key), 363, fig. 3. Fincham, 1987, p. 353 (key).
Macrobrachium handschini – Bruce, 1992, pp. 131–139, figs 1–5.

Material examined

Paralectotype. *Northern Drainage Region. Daly R Basin*: NTM Cr007117, Katherine, R., N.T.

Holotype of *Macrobrachium glypticum* Riek, 1951. *Northern Drainage Region. Archer R Basin*: AM P11992, male, Coen, Qld.

Other material: Northern Drainage Region. Victoria R Basin: NTM Cr012774, Victoria R.; *Daly R Basin*: WAM C11531, Katherine R.; *South Alligator R Basin*: NTM Cr007394, Jim Jim Ck Falls, Kakadu N.P.; *Roper R Basin*: SAM C5858, Roper R. near Mataranka; NMV J21541, Roper R.; QM W8589, Flying Fox Ck, Mountain Valley Stn; QM W9718, Wilton R.; *Robinson R Basin*: QM W12595, Robinson R.; NTM Cr007390, Robinson R. crossing; *Calvert R Basin*: NTM Cr007411, Karns Ck, junction with Calvert R.; *Nicholson R Basin*: QM W12613, Gregory R., Riversleigh Stn; SAM C5859, Beames Brook, 37.5 km north of Gregory Downs Stn on Burketown Rd; QM W20650, Lawn Hill Ck, Lawn Hill N.P., just above upper Gorge; QM W20663, Louie Ck, tributary of Lawn Hill Ck, Lawn Hill N.P.; *Norman R Basin*: QM W14939, Norman R., Normanton-Karumba Rd; *Mitchell R Basin*: QM W16632, Rifle Ck near Mt Molloy; QM W16091, Mitchell R.; *Archer R Basin*: QM W16694, Lankelly Ck, Coen; QM W11971, Coen R.; QM W16697, Archer R., Peninsula Developmental Rd crossing; QM W16392, Archer R.; *Wenlock R Basin*: QM W19658, Wenlock R.; QM W16699, Wenlock R., Peninsula Developmental Rd cross-

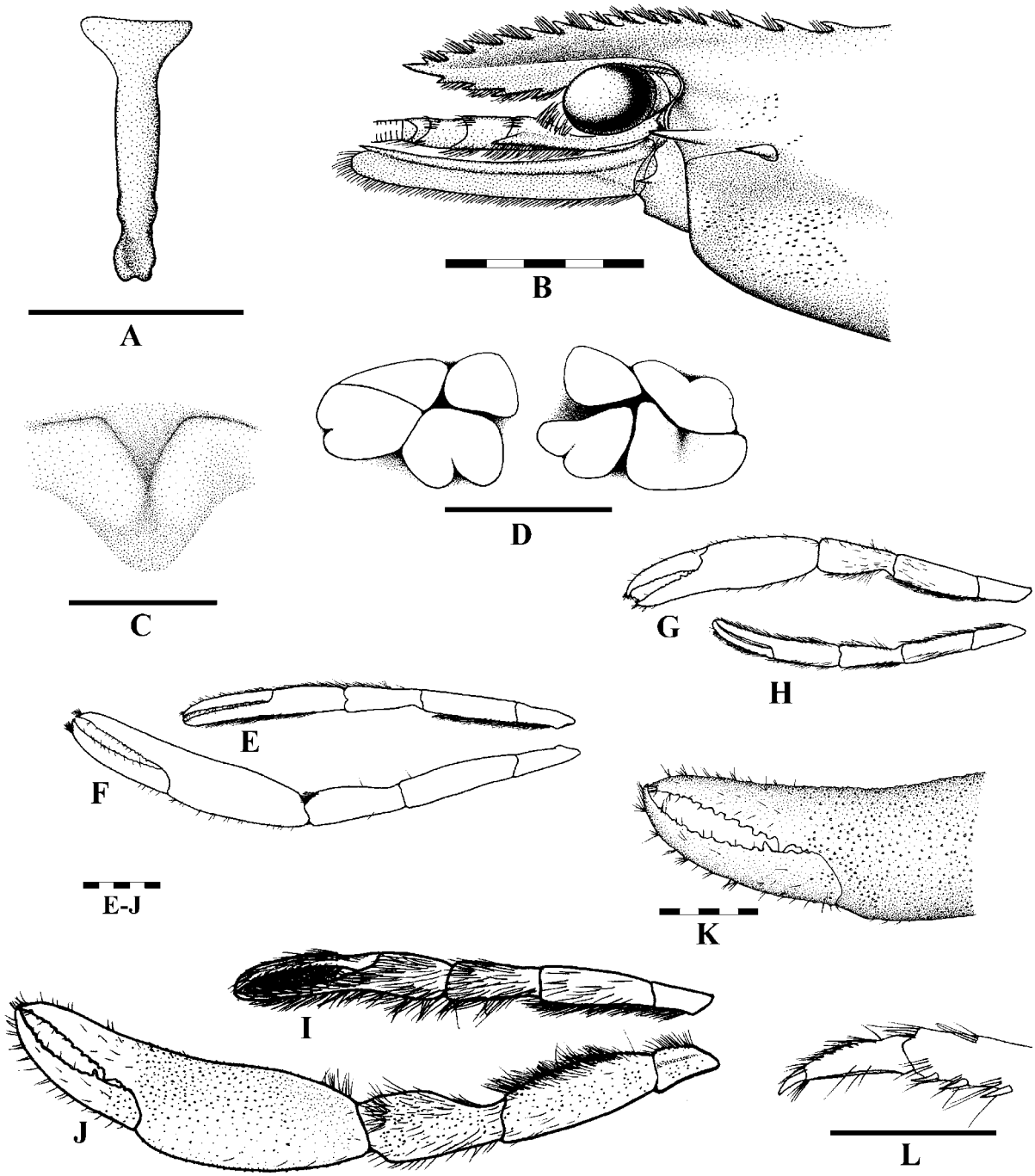

Figure 33. Macrobrachium handschini (Roux, 1933). (A) QM W14939, male 16.1 mm CL, inter-uropodal sclerite, (B) QM W16091, male 11.9 mm CL, anterior cephalothorax, (C) QM W20663, male 16.9 mm CL, epistome, (D) Crowns of left and right mandibular molar processes (setae omitted), (E) QM W20663, male 12.6 mm CL, undeveloped minor second cheliped (protective setation omitted), (F) Undeveloped major second cheliped (protective setation omitted), (G) QM W20663, ovigerous female 10.6 mm CL, undeveloped major second cheliped (protective setation omitted), (H) Undeveloped minor second cheliped (protective setation omitted), (I) QM W20663, male 14.8 mm CL, fully developed minor second cheliped (protective setation omitted), (J) Fully developed major second cheliped of same, (K) fingers and distal manus of fully developed major cheliped of same, (L) Dactylus and distal propodus of fully developed right third pereiopod. Solid scale bars and divisions on divided scale bars 1 mm.

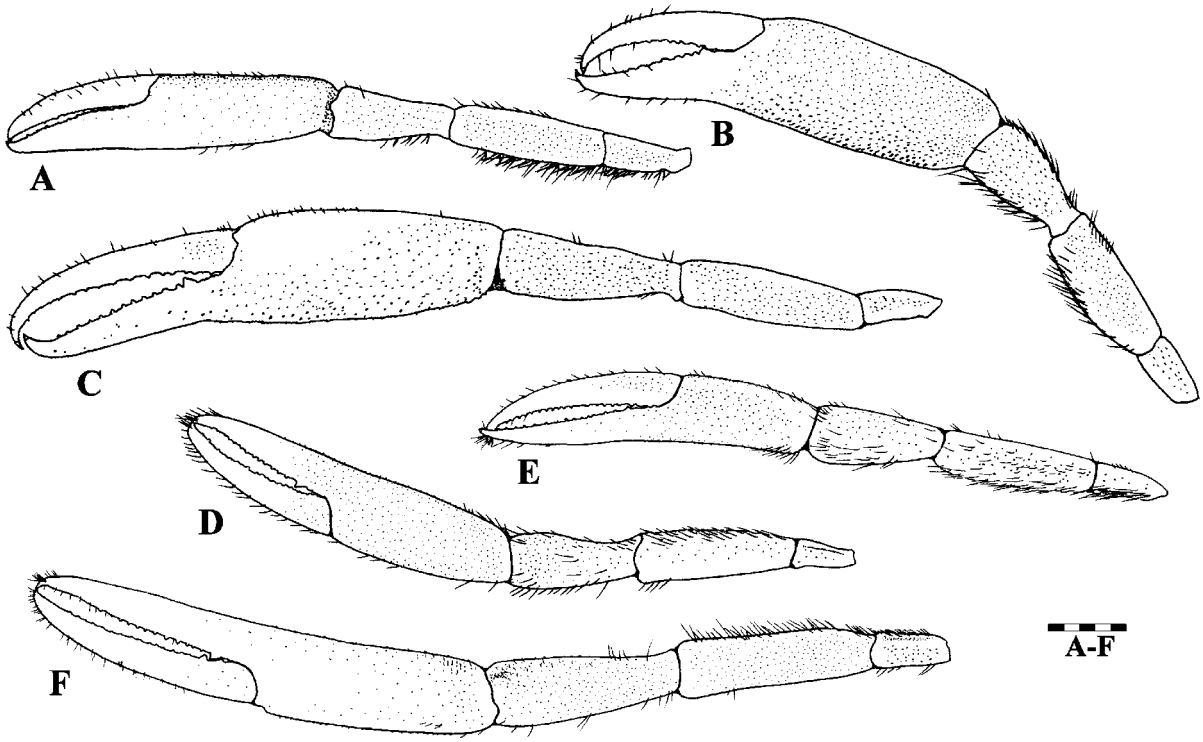

Figure 34. Macrobrachium handschini (Roux, 1933), developed major chelae. (A) QM W22244, male 17.4 mm CL, Kamora R., Timika area, southern Irian Jaya, (B) NMV J21541, male 13.8 mm CL, Roper R, (C) QM W20021, male 14.2 mm CL, Fly R. at Obo Stn, Papua New Guinea, (D) QM W20663, male 15.9 mm CL, Louie Ck, Lawn Hill N.P., Qld, (E) Same lot, male 16.2 mm CL, (F) SAM TC 11160, male 18.6 mm CL, Roper R. at Mataranka, NT. Scale bar divisions 1 mm.

ing; QM W16850, Wenlock R., Stones Crossing; QM W16703, Dulhunty R., telegraph line crossing; *Ducie R Basin*: QM W16391, Cockatoo Ck; *Jardine R Basin*: QM W8858, Jardine R.

Eastern Drainage Region. Jacky Jacky Ck Basin: QM W16808, Harmer Ck near Shelburne Stn hmstd; *Normanby R Basin*: QM W16634, Normanby R., Orange Plain Waterhole; QM W16903, Normanby R., Battle Camp-Cooktown Rd crossing; QM W16690, Hann R. near Hann R. roadhouse; QM W15024, Kennedy R., Hann Crossing.

Papua New Guinea: QM W20021, Fly R. at Obo Station; QM W20022, Suki Ck, Fly R. catchment.

Irian Jaya: QM W22244, Kamora R., Timika area, southern Irian Jaya.

Diagnosis

Rostrum. Short in fully developed males, developmental range 0.5–0.6 CL; moderately deep (maximum depth slightly more than dorsoventral diameter of eye); dorsal carina convex, dentate along entire length, teeth subequally spaced, 9–15 teeth, 3–4 completely postorbital, number of proximal teeth submoveable in developed males; ventral carina dentate, 2–5 teeth, first tooth generally located well within proximal half.

General cephalon. Ocular cornea large, well-pigmented, accessory pigment spot present. Inferior orbit moderately produced, obtuse, post-antennular carapace margin evenly rounded. Bec ocellaire moderately developed. Scaphocerite stout, length less than three times maximum breadth, lamina distinctly tapering from broadest point to anterior margin, anterior margin produced forward at inner angle. Epistome completely divided into two lobes, lobes produced anteromesially.

Mouthparts. Third maxilliped terminal segment clearly shorter than penultimate segment; exopod slightly shorter than to about equal in length to

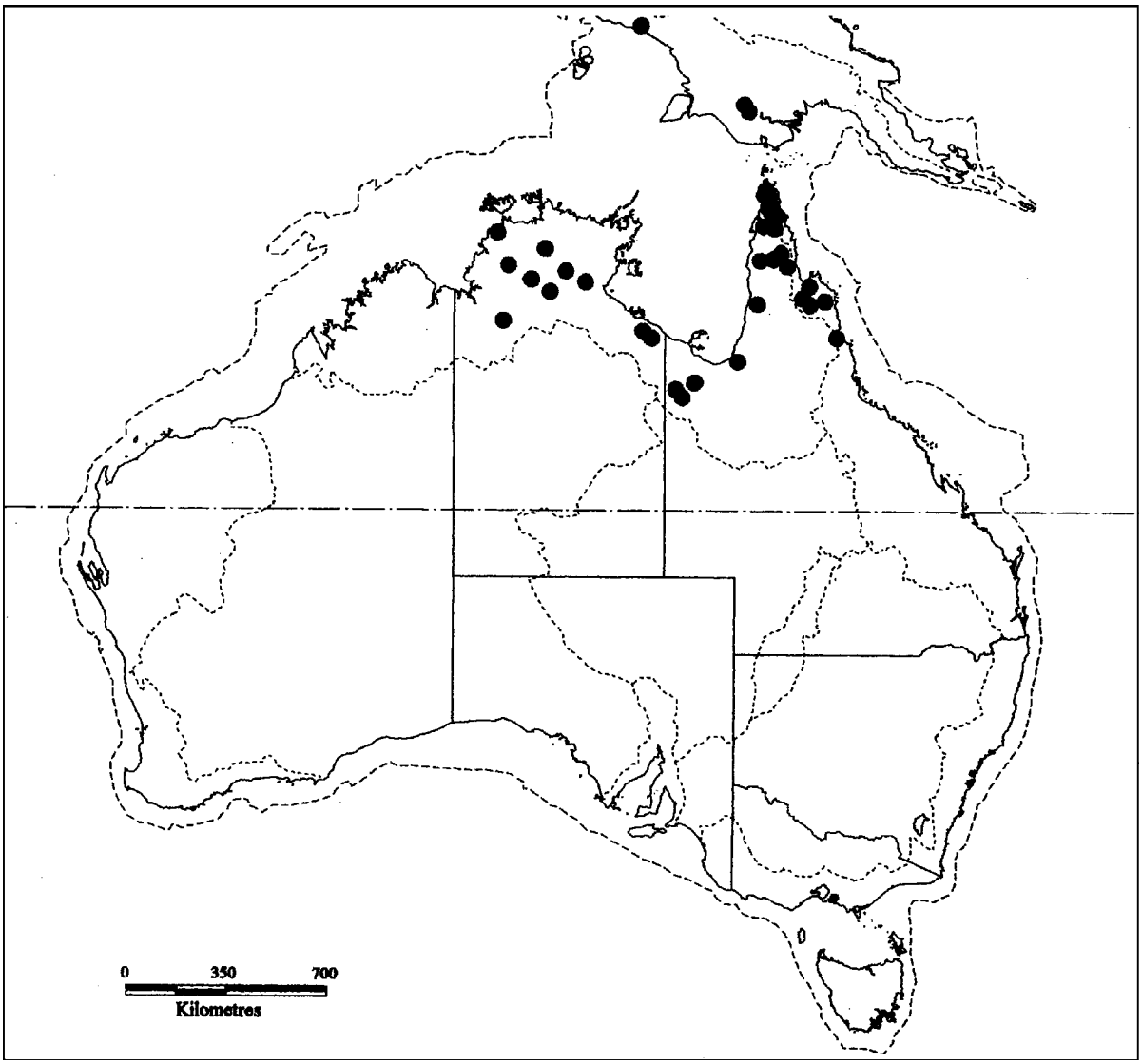

Figure 35. Distribution of *Macrobrachium handschini* (Roux, 1933).

ischiomerus. Mandibular molar process crowns as figured (Fig. 33D).

Second chelipeds (fully developed male). Larger and more developed than female P2; fully dimorphic; short, carpus or more distal segments of minor cheliped reaching distal end of scaphocerite; major cheliped bearing protective, simple and multidenticulate setae; abundant erect mamilliform protective setae on ischium, merus and carpus, more sparsely distributed on chela except for lateral face of manus; multidenticulate setae most abundant on inferior ischium and merus, also present on inferior carpus, largely absent on chela; fingers with well developed gape; pollex strongly tapered from markedly broadened base, clearly broader than basal dactylus, cutting edge more or less straight, bearing dentate ridge proximally followed by incisor tooth then series of rounded well-spaced teeth, teeth diminishing in size distally; dactylus often arched, cutting edge dentition similar to pollex except incisor tooth generally smaller and slightly advanced of corresponding tooth on pollex; manus broad, maximum breadth much greater than maximum merus breadth, much

longer than dactylus; carpus clearly shorter than chela, tapered, inflated (particularly from Gregory River west); merus distinctly shorter to slightly longer than carpus, cylindrical, inflated (particularly from Gregory River west); ischium very short, compressed, tapered to subrectangular, with well developed medial groove and broad depression on superior face.

Minor cheliped differing from major cheliped in having relatively smaller protective setae on ischium, merus and carpus, and relatively few protective setae on manus; all segments with multidenticulate setae, abundant on inferior ischium and merus, forming well-developed inwardly-directed brushes on cutting edges of fingers; fingers with weak gape; pollex slender, very slightly curved mesially, not noticeably broadened basally, cutting edge with number of small teeth proximally followed by oblique carina, carina terminating submedially and lateral to unguis; dactylus slender, slightly curved mesially, cutting edge with number of small teeth proximally followed by median carina; manus much shorter than dactylus, maximum breadth slightly greater than or c. equal to maximum merus breadth; carpus tapered, slightly inflated distally; merus c. equal in length to clearly longer than carpus, cylindrical in distal half, compressed proximally.

Third pereiopods (fully developed male). Short, failing to reach distal end of scaphocerite; protective setation absent; dactylus of medium length, length c. four times basal breadth, ventral carina well developed; unguis strongly developed, c. one-third length of remainder of dactylus.

Thoracic sternum. T4 with well-developed median process, postcoxal flanges situated posterior to and distinct from median process. Fully developed male T8 with anterolateral lobes contiguous posteromedially, without median process posteriorly.

Abdomen. Inter-uropodal sclerite without preanal carina. Distolateral process on uropodal exopod with accessory spiniform seta mesially.

Body setation (fully developed male). Spiniliform protective setae present on anterolateral carapace only, absent on abdomen.

Colour

Antennal flagella olive grey to yellow brown, scaphocerites translucent, tinged with olive grey to olive brown, peduncles mottled with blue grey to olive brown. Rostrum with dorsal and ventral carinae translucent, tinged with blue grey to olive brown, lateral carina mottled with blue grey to olive brown. Body mottled with blue grey to olive brown, sometimes almost uniformly coloured in fully developed males.

Body bluish-grey to reddish-brown with light transverse band on third abdominal tergite; major cheliped bluish-brown except for blue fingers with white tips; minor cheliped reddish-brown, finger tips white.

Ambulatory legs indistinctly banded with bluish grey, orange brown and cream bands. Second chelipeds drab grey merging into blue grey or olive brown, with light coloured finger tips, sometimes mottled with dark blotches on manus and fingers, lighter areas overlaid with reticulated pattern.

Life cycle

Restricted to fresh waters, eggs moderately large and few, 13–68 per brood, maximum length of developed ova 1.5 mm. Larval development unstudied, size of developed ova and the form of the first larval stage indicative of highly abbreviated type. First larval stage moderately large, robust, c. 3 mm total length; eyes sessile; rostrum short, downturned, entire; telson broad posteriorly with numerous plumose setae, uropods absent; 5 pairs of non-setose, but well-developed pleopods; all thoracopods present; maxillipeds with long natatory exopods, all pereiopods well developed with shorter non-setose exopods; P1-2 subchelate.

Size

Small species: Maximum size of developed male 19 mm CL, 63 mm TL. Maximum size of female 12 mm CL, 37 mm TL, minimum size of ovigerous female, 6.4 mm CL.

Habitat ecology

Recorded from spring-fed, perennially-flowing streams and seasonal watercourses in billabongs, lagoons and waterholes. The altitudinal distribution of the species extends from coastal lowlands to upper catchment tributaries (up to 300 m ele-

vation). Substrates: medium to coarse particle size including sand, gravel and rocks, also bedrock. Flow: zero to high. Water clarity: generally high during dry season. Water depth: 0.02–1.5 m. Recorded physico-chemical tolerances: water temperature 24–28 °C (field, $n = 2$), pH 6 (field, $n = 4$). Fringing vegetation: open communities dominated by *Eucalyptus*, *Melaleuca*, and *Pandanus* to closed monsoon forest.

Behaviour

Prefers to shelter in leaf litter beds (often in shallow water), or underneath fallen timber or rocks.

Distribution

Southern New Guinea and northern Australia. Australian distribution: Victoria R. basin, N.T. to Normanby R. basin, Qld.

Systematic position

The differences between *M. handschini* and the closely related species, *M. latidactylus*, have been discussed above under the latter species. *M. handschini* also shows affinities to *M. bariense* (De Man, 1892) and *M. papuanum* (Roux, 1927). The latter species was originally described as a subspecies of *M. oenone* but lacks the characteristic anastomising grooves on the major chela and deserves full species rank.

M. handschini differs from both *M. bariense* and *M. papuanum* in having much larger ova – 1.5 mm maximum length vs. 0.5–0.7 mm in the latter two species. *M. bariense* also can also be separated from *M. handschini* by the absence of a median process on thoracic sternite 4 and the lack of protective setation on the minor cheliped in fully developed males.

Vernacular names

Handschin's river prawn.

Remarks

As noted by Bruce (1992), the original description by Roux (1933) from the Katherine River, N.T., was brief and unillustrated. In Holthuis's (1950) monograph on the Palaemoninae collected by the Siboga and Snellius Expeditions with remarks on other species, this species was placed among 'species incertae'. Although thoroughly re-described by Bruce (1992), the designated lectotype is clearly an undeveloped male specimen, as are the five remaining paralectotype males.

The above diagnosis is based on an examination of over 170 specimens, including many developed males, from the Daly R. basin, N.T. (which includes the type locality) through to the Normanby R. basin in northeast Qld. There is a general tendency for Northern Territory and western Queensland specimens to have shorter more inflated chelipeds with strongly gaping fingers. Variation within populations may exceed this geographic trend however (Fig. 20).

The holotype of *M. glypticum* Riek, 1951, described from Coen, Cape York Peninsula is a developing male of this species. Riek (1951) was apparently unaware of the description of *Palaemon* (*Macrobrachium*) *handschini* Roux, 1933 and did not include the taxon in his account of Australian freshwater species.

Discussion

The Australian fauna now comprises 13 species, five of which are endemic to the continent and associated continental shelf islands. Of the five endemics, three are large-egged, land-locked, freshwater species, while the remaining two have small eggs and a euryhaline life cycle. Only one species is endemic to Australia and southern New Guinea, viz. the land-locked, freshwater species, *M. handschini*.

The level of endemicity of the Australian fauna is significantly higher than other large islands in the Indo-West Pacific, with the exception of Borneo, and is more typical of a continental fauna. Islands such as Hawaii, Fiji, New Caledonia, Sumatra, the Philippines, Taiwan, Timor, Madagascar and the main islands of Japan have very low levels of endemicity and are typically inhabited by wide-ranging euryhaline species. The large land area, stable geological history and relative isolation of the Australia continent appear to have been important contributors to the high level of ende-

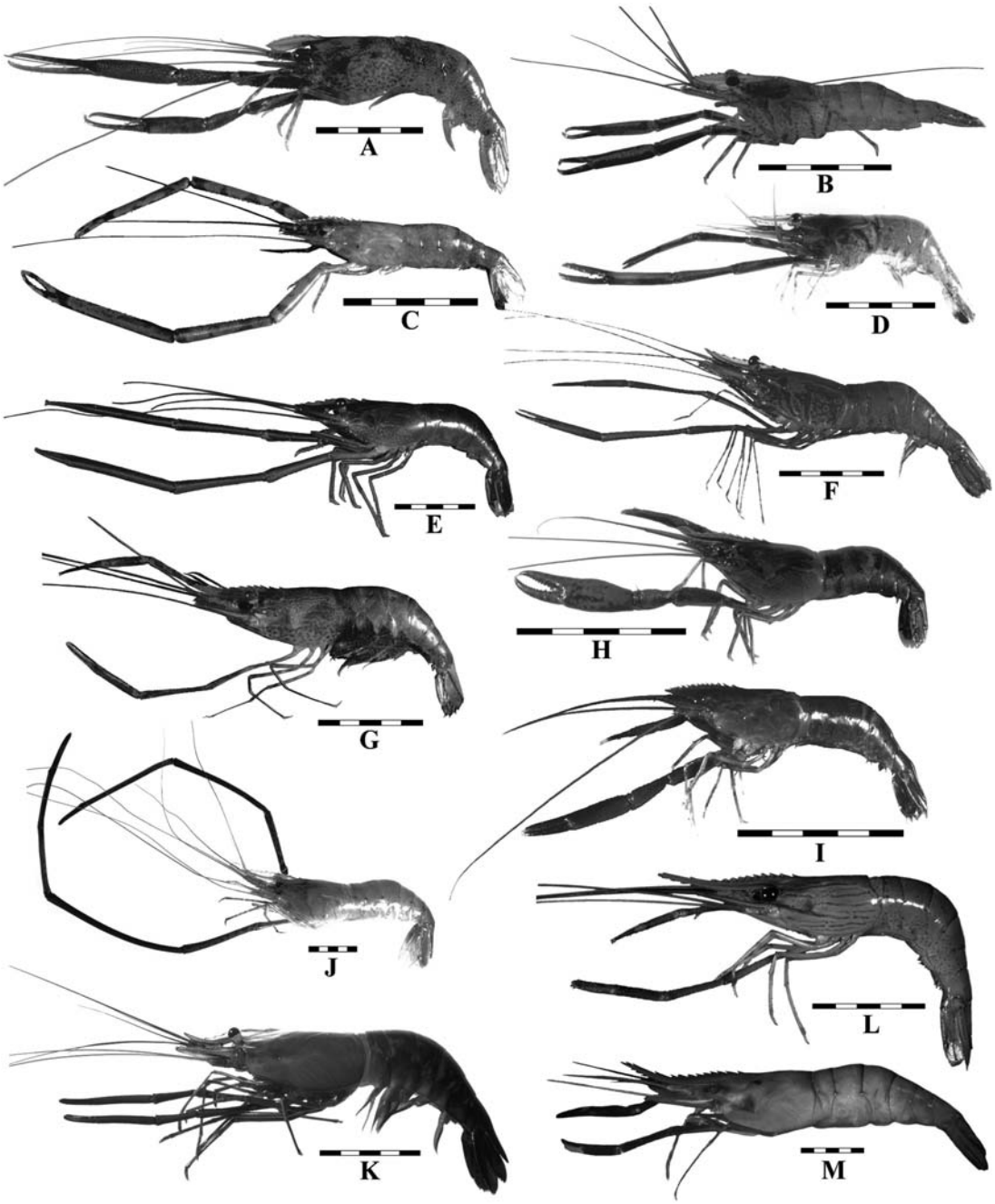

Figure 36. Chromatophore patterns of Australian *Macrobrachium*. (A) *M. koombooloomba* sp. nov., QM W18128, developed male paratype, (B) *M. bullatum* Fincham, 1989, developed male, Litchfield N.P., N.T. (digitally enhanced from photograph supplied by Northern Territory Museum of Arts and Sciences), (C) *M. auratum* sp. nov., QM W18283, developed male paratype, (D) *M. australiense* Holthuis, 1950, QM W18265, developed male, (E) *M. tolmerum* Riek, 1951, QM W16800, developed male, (F), *M. idae* (Heller, 1862), QM W18233, developing male, (G) *M. equidens* Dana, 1852, QM W16750, ovigerous female, (H) *M. handschini* (Roux, 1933), QM W20663, developed male, (I) *M. handschini* (Roux, 1933), QM W16850, developed male, (J) *M. novaehollandiae* (De Man, 1908), QM W15519, developed male, (K) *M. lar* (Fabricius, 1798), QM W21490, undeveloped male, (L) *M. rosenbergii* (De Man, 1879), QM W22028, young adult female, (M) *M. rosenbergii* (De Man, 1879), QM W16848, immature female. All scale bars 25 mm, divisions 5 mm.

micity and the presence of land-locked freshwater species.

The total number of species occurring on the Australian continent compared to the total land area is less impressive. In global terms, the level of diversity is quite high, i.e. comparable to the whole East Pacific and East Atlantic faunas, but is low compared to other large land areas in the rich Indo-West Pacific region. The Indian subcontinent which has less than half the total land area has almost three times as many species. New Guinea has at least eight more species but less than one-tenth of the land area.

The lack of reliable rainfall over a large part of the continent both in present times and during glacial periods of the Pleistocene has probably been significant in the low level of species diversity. The relatively flat, featureless topography of the Australian continent is also likely to be important. Much of the arid and semi-arid interior is extremely flat by world standards. The most extensive area of dissected topography in Australia, the Kimberley Plateau, experiences highly seasonal rainfall.

Along the east coast, highland regions are also typically inhabited by the parastacid crayfish genus, *Euastacus*. In drainages where *Euastacus* occur, *Macrobrachium* are largely restricted to lower elevations, suggesting that *Euastacus* may competitively exclude *Macrobrachium*. By contrast, highland habitats in Asia are devoid of crayfish and contain a high number of unique *Macrobrachium* species.

There is also evidence that Torres Strait and the Timor, Arafura and Coral Seas remain effective dispersal barriers restricting the entry of wide-ranging Indo-West Pacific species into Australia. The absence of *M. australe* and *M. latimanus*, both of which occur in southeast New Guinea, is particularly interesting. It is possible that one or both of these species may eventually be found in northeast Australia, particularly in the Wet Tropics region between Cooktown and Townsville.

Also notably absent from the Australian *Macrobrachium* fauna are obligate cave species, despite the existence of a diverse hypogeal atyid fauna in northern Australia. Extensive cave systems containing permanent water exist in the Northern Territory, the Kimberley region of Western Australia and in northwest Queensland. It is likely that one or more species of *Macrobrachium* will eventually be found among these areas with more intensive collecting.

Present distribution patterns suggest that wide-ranging species have commonly entered Australia via eastern Cape York Peninsula. Northeast Queensland has by far the highest diversity of species and only the northwest Australian, *M. bullatum*, is absent from the region. Clinal variation in the morphology of *M. rosenbergii* also supports this hypothesis. This species shows increasing morphological divergence from the typical New Guinean form of the species as you progress westward across Northern Australia. The Kimberley region of northwest Australia is also highly depauperate compared to northeast Queensland and contains only five species. Species diversity also declines dramatically on the east coast below the Tropic of Capricorn, with only four species occurring between Rockhampton and Sydney. The most impoverished region in Australia is the arid and semi-arid interior. Only one widely distributed, adaptable species, *M. australiense*, has colonised the Murray-Darling and Lake Eyre drainage divisions.

In northeast Queensland, where species diversity is highest, up to 10 species may be found in a single river system. In the lower freshwater reaches it is not uncommon for four or five species to occur together at the same locality. Without obvious differences in mouthpart morphology and feeding strategies (all appear to be opportunistic omnivores) it is at first puzzling how so many species can coexist. In part, sympatric species are able to share the same body of water through habitat partitioning e.g. different shade, water flow and depth preferences. For example, *M. auratum* sp. nov. is able to live under rocks in open areas of very shallow water, particularly in riffles. By contrast, *M. lar* prefers well-oxygenated, heavily-shaded habitats with abundant shelter, often immediately below riffles or glides.

Australian *Macrobrachium* also show a wide variety of dispersal behaviour, life history traits and salinity tolerance. These in combination determine the longitudinal distribution of species within a watercourse and tend to limit direct competition between species. The highest degree of distributional overlap and highest species diversity

Figure 37. (A) Crystal Ck, NE.Qld. Perennially flowing, riverine habitat of *Macrobrachium auratum* sp. nov. (B) Elliott R. at Guthulungra, ME.Qld. Seasonally-flowing, sandy, riverine habitat of *Macrobrachium auratum* sp. nov. (C) Perennially-flowing creek on Koombooloomba Rd near Koombooloomba Dam turnoff, upper Tully River basin, NE.Qld. Type locality of *Macrobrachium koombooloomba* sp. nov. at ecotone between simple notophyll fern forest and open sclerophyll forest, (D), Perennially-flowing tributary of O'Leary Ck, upper Tully River basin, NE.Qld. Simple notophyll fern forest habitat of *Macrobrachium koombooloomba* sp. nov.

tends to occur in the lower freshwater reaches near the upstream limit of tidal influence.

Based on their life history, longitudinal distribution, dispersal behaviour and salinity tolerance, Australian species can be conveniently divided into five ecological groups. These groups are also applicable through the range of the genus and are largely equivalent to those utilised by Storey et al. (2000) for species in the Fly River system, Papua New Guinea.

Group 1 is comprised of estuarine euryhaline species with distributions extending upstream as far as the limit of tidal influence and with lengthy estuarine-marine larval development. Species of this group probably have a lifestyle similar to ancestral species of the genus. In Australia, the group is represented by *M. equidens* and *M. novaehollandiae*. Both species are widely distributed across northern Australia, although *M. equidens* also has an extensive distribution elsewhere in the Indo-West Pacific. Although the two species appear related they are highly conservative in morphology and do not share any unique characters.

Group 2 contains lowland euryhaline species with limited upstream dispersal into non-tidal fresh waters. Lengthy estuarine-marine larval development is typical of this group. Adults are amphidromous and are commonly found in both brackish waters and the lower freshwater reaches of major rivers and coastal streams. This group represents the first step in the invasion of freshwater habitats. Three species show this distribution pattern in Australia, viz. *M. idae*, *M. latidactylus* and *M. mammillodactylus*. Both *M. latidactylus* and *M. mammillodactylus* have wide distributions in the Central Indo-West Pacific whereas *M. idae* has an even broader distribution pattern extending from East Africa to the Philippines, New Guinea, and Australia. In Australia, all three species are restricted to northeast Queensland. This is the dominant ecological group in the genus and has many representatives in other parts of the world.

Like the Australian Group 1 species, to which they appear related, *M. idae* and *M. mammillodactylus* are highly conservative in morphology and show comparatively few derived characters. By comparison, *M. latidactylus* appears more highly evolved and closest to the land-locked, freshwater species, *M. handschini*.

Group 3 is comprised of widely distributed, euryhaline species with broad longitudinal distributions from lower estuary to middle or upper catchment. Characteristically, species of this group have very high fecundity, lengthy estuarine-marine larval development and well-developed upstream dispersal behaviour as juveniles or adults. Adult females may be catadromous (migrate to brackish water to spawn) or rely on river flow in the lower freshwater reaches to transport larvae to tidal waters. This group represents a further step in the progressive colonisation of fresh waters by the genus. In Australia, this is the most common distributional/reproductive strategy and is shown by four species – *M. lar*, *M. rosenbergii*, *M. tolmerum*, and *M. auratum* sp. nov. The first of these species, *M. lar* has the broadest distribution of any species in the genus and occurs throughout a larger part of the Indo-West Pacific from East Africa to Micronesia and French Polynesia. Like the last two species, *M. lar* appears to rely on river flow to transport larvae down to the estuary. The second species, *M. rosenbergii* has a wide distribution in the Central Indo-West Pacific from Pakistan to Taiwan, Palau, New Guinea and Australia. This is generally a catadromous species and annual breeding migrations of adult females from freshwater to estuarine areas have been observed by a number of workers (Rao, 1967; George, 1969). The last two species are endemic to eastern Australia. Of the two endemics, *M. tolmerum* has stronger upstream dispersal behaviour and is capable of scaling major waterfalls. Of the Australian species in this group, only *M. tolmerum* and *M. auratum* sp. nov. appear closely related.

Group 4 contains widely distributed freshwater species with relatively broad habitat preferences and wide longitudinal distributions from the upstream limit of tidal influence to upper catchment. Larval development is at least partially abbreviated and fecundity varies from low to moderately high. Species of this group represent the penultimate stage in the colonisation of fresh waters. Although group 4 species no longer require tidal influence for larval development, they still have broad habitat preferences and wide altitudinal distributions. Three Australian species show this pattern, viz. *M. australiense*, *M. bullatum*, and *M. handschini*. Both *M. australiense* and *M. bullatum* appear capable of climbing major physical

barriers such as waterfalls and have distributions extending into upper catchment areas. Locality records of *M. handschini* suggest that it does not extend as far upstream.

Australian representatives of this group show a number of derived features but do not appear to represent a monophyletic group. It is likely that each has evolved from a different euryhaline ancestor e.g. *M. bullatum* appears allied to *M. mammillodactylus*, *M. handschini* is closest to *M. latidactylus*, and *M. australiense* may be related to *M. equidens* or *M. idae*.

Group 5 species have a restricted freshwater distribution pattern and specialised habitat requirements. Typically, they also have low fecundity and abbreviated development. Usually, they are associated with specific flow regimes/water chemistry and or isolated topography e.g. above a major waterfall or in caves. Species of this group show the highest degree of divergence away from an ancestral euryhaline lifestyle and represent the final stage in the progressive colonisation of fresh waters. Only one Australian species, *M. koombooloomba* sp. nov. is representative of this category. This is the most distinctive, and in all probability, the most highly-evolved, Australian species.

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