The first British record and a new species of the superfamily Terrestricytheroidea (Crustacea, Ostracoda): morphology, ontogeny, lifestyle and phylogeny

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***Terrestricythere elisabethae* sp. nov.** is described from a semiterrestrial coastal habitat at two sites in Hampshire, southern England. It is the first record of a living population of the genus outside the Far East (north-west Pacific). Based on extensive collections and from observations of cultures, its morphology is described (including a formal definition of the unique 'visordont' hinge), as well as its ontogeny and lifestyle (encompassing habitat, life cycle, mode of life and locomotion). A further new species from Somerset, south-west England is also recorded on the basis of a single specimen but left in open nomenclature. The affinities of the Terrestricytheroidea are discussed in the context of a tentative phylogeny of podocopan Ostracoda. Both carapace and appendage characters are such as to warrant maintaining it as a separate superfamily, which is more closely related to the Cytheroidea and Darwinuloidea than to the Cypridoidea.   © 2004 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2004, **142**, 253–288.

ADDITIONAL KEYWORDS: brackish – Bristol Channel – English South Coast – leaf litter – new species – semiterrestrial – *Terrestricythere* – **T. elisabethae** sp. nov. – tidal creek.

INTRODUCTION

A limited number of taxa of the predominantly aquatic Ostracoda are known to live in semiterrestrial and terrestrial habitats such as damp mosses, soil and leaf litter. All but one of these belong to the podocopid superfamilies Cypridoidea (Klie, 1939; Harding, 1953, 1955; Danielopol & Betsch, 1980; Schornikov, 1980; De Deckker, 1983) and Darwinuloidea (Danielopol & Betsch, 1980; Schornikov, 1980; Pinto, Rocha & Martens, 2003). With these affinities they may be assumed to have originated in freshwater environments. The superfamily Terrestricytheroidea is unique in having apparently invaded coastal terrestrial habitats directly from marine/brackish environments. Although the lineage is so far represented by only a single genus, *Terrestricythere* Schornikov, 1969, containing two living species (no fossil examples have yet been recognized), its morphological characteristics render it quite distinct from other podocopid superfamilies and are suggestive of considerable antiquity. Here we present the first records of *Terrestricythere* in the British Isles and formally describe a new species. A second undescribed British species, represented by a single specimen, is left in open nomenclature.

Schornikov (1969) described the new genus and species *Terrestricythere ivanovae* on the basis of a collection of 85 specimens from the supralittoral zone of Iturup Island in the Kurils (north-west Pacific), recognizing sufficient distinguishing features to merit the establishment of a new family, the Terrestricytheridae. It was found living among small pebbles that are kept constantly damp by mist, rain and sea spray. Subsequently a second species, *T. pratensis,* was

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described by the same author (Schornikov, 1980) from a monsoonal salt marsh with brackish groundwater at a coastal site in Primorski Territory, Russian Island (Amur Gulf) near Vladivostok; a second population of *T. ivanovae* was discovered at the same general location, among supralittoral salt-tolerant plants and littoral filamentous algae, about 20 m from where *T. pratensis* was found.

Our first encounter with the genus was the discovery of a single individual in a collection of intertidal rockpool ostracods from Gore Point, near Porlock on the southern shore of the Bristol Channel (south-west England). It was identified by two of us (DJH and JEW) in 1978 as an adult male *Terrestricythere* that could not be assigned to either of Schornikov's species. However, since neither subsequent searches of possible intertidal and supratidal habitats in the vicinity, nor a comprehensive seasonal sampling of intertidal algae for ostracods at Gore Point (the latter constituting PhD research by DJH) produced any further examples, it was considered probable that the single male had been accidentally introduced and the record remained unpublished.

Years later, one of us (JWM) obtained some unusual ostracods while collecting salt marsh Foraminifera with his Norwegian colleague, Elisabeth Alve, on the River Cur, a tidal tributary of the Hamble Estuary, Hampshire, southern England. They were immediately recognized as *Terrestricythere* by JEW. Here we present details of this find, which we believe to be the only living populations of *Terrestricythere* that are known outside the north-west Pacific region.

There is one previously published European record of the genus. Scharf & Keyser (1991) reported two specimens, an adult male and a juvenile, from Lac du Bouchet in the Massif Central of France. We are grateful to the authors for a copy of a plate (which was never actually published) showing scanning electron micrographs of both the adult from Lac du Bouchet and a specimen from Schornikov's Kuril Islands collection, which leaves us in little doubt that their identification of the French specimens as *T. ivanovae* is correct. Scharf & Keyser considered the presence of an adult and a juvenile to indicate that a living population was present. In our view, however, given the difference in habitat (a freshwater lake, compared with the marine-influenced semiterrestrial habitats in which *Terrestricythere* species have normally been found), it is more likely that their two specimens represented another accidental, one-off introduction.

Having studied the habitat of *Terrestricythere* on the Hamble we searched for similar habitats along the Beaulieu River Estuary, about 15 km further west, on the other side of Southampton Water, and discovered populations of the same species on the margins of two creeks at Jarvis Copse and Bailey's Hard. We have searched similar habitats in southern England around Poole Harbour and on the Isle of Wight, and in northern England on the Leven Estuary (Morecambe Bay), although without success. The Bristol Channel locality is rather different, with an open rocky shore and only a small area of salt marsh and creeks in the shelter of a shingle beach. Recent deliberate searches of possible habitats on two occasions (subsequent to our discovery of the Hamble population) have failed to yield any more specimens.

The *Terrestricythere* from the Hamble Estuary and Beaulieu River Estuary differs in several important respects from Schornikov's two species, and is accordingly described herein as new. The example from the Bristol Channel appears to represent a fourth species of the genus, here left in open nomenclature, as we are reluctant to describe a new species on the basis of a single specimen.

MATERIAL AND METHODS

Specimens were obtained by washing wet leaf litter, collected from the banks of a small tidal creek among reed beds, through 2.0 mm and 0.075 mm sieves, the ostracods being retained on the smaller mesh size. The appendages were dissected and mounted in Hydromatrix (a water-based mounting medium based on polyvinyl alcohol) on glass slides and drawn with the aid of a camera lucida. Soft parts for SEM investigation were critical point dried. Carapaces studied for internal views were cleaned using 7% solution of KOH (potassium hydroxide), mounted on stubs and sputter coated with gold-palladium, prior to being viewed using a Hitachi S2500 scanning electron microscope. Cultures were kept and the movements of live specimens (both from above and from below through a glass slide) were studied in the laboratory with a high-resolution video-microscope and recorded on S-VHS video tape. All figured material is registered in the Department of Zoology, The Natural History Museum, London, UK [BMNH 2003.979–1049].

Terminology for figures and descriptions
An1 – antennula; An2 – antenna; Md – mandible; Mx – maxillula; L5 – fifth limb; L6 – sixth limb; L7 – seventh limb; Fu – furca (comprising a pair of furcal rami); Ab – abdominal seta; Hem – hemipene; LV – left valve; RV – right valve.

TAXONOMIC DESCRIPTIONS

CLASS OSTRACODA LATREILLE, 1806
ORDER PODOCOPIDA SARS, 1866
SUBORDER CYTHEROCOPINA GRÜNDEL, 1967
SUPERFAMILY TERRESTRICYTHEROIDEA SCHORNIKOV,
1969 [*NOM. TRANS.* HARTMANN & PURI, 1974]
FAMILY TERRESTRICYTHERIDAE SCHORNIKOV, 1969
GENUS *TERRESTRICYTHERE* SCHORNIKOV, 1969

Type species: *Terrestricythere ivanovae* Schornikov,
1969: 495–497, figs 1–16.

Diagnosis
Carapace with curved dorsal margin, LV larger than
RV. LV with small lobe-like extension overlapping RV
towards anterior margin. Hinge 'visordont' (see sec-
tion titled 'The hinge of *Terrestricythere*', below, for for-
mal definition), with two teeth on RV situated towards
anterior and posterior margins and joined by ridge
running along dorsal margin. Lobes interlock and
rotate in two pits on hinge of LV so that LV dorsally
overrides RV. Basic adductor muscle scar pattern of
five in approximately vertical row, second and third
from bottom diagonally offset from each other (second
displaced anteriorly, third posteriorly, from imaginary
vertical centre line). Antennula with five or six artic-
ulated podomeres. Antennal exopodite a plate with
seven or eight long setae. Mandibular palp with rake
setae and branchial plate with one ray. Female fifth
limb endopodite with three articulated podomeres;
modified into clasping palps in males. Sixth limb with
four robust podomeres, with a series of short claws
and setules along anterior edge. Seventh limb with
five podomeres, terminating in two slender, hooked
claws, one longer than the other. Furcal rami each
reduced to three small setae. Eye absent.

TERRESTRICYTHERE ELISABETHAE SP. NOV.
(FIGS 1–17, 21, 25, 26)

Type locality
Tidal estuary of the River Cur (tributary of the
Hamble Estuary) Hampshire, UK, 50°54′09.1″N,
1°15′14.4″W; oak leaf and reed litter overlying mud in
the high intertidal zone reed marsh.

Type material
Holotype: a male, with soft parts dissected in Hydro-
matrix and sealed in a glass slide (No. 2003.1025). Col-
lected 2 May 2002.

Allotype: a female, with soft parts dissected in Hydro-
matrix and sealed in a glass slide (2003.1023).

Paratypes: two males with soft parts dissected in
Hydromatrix sealed in a glass slide and valves stored
in a cavity slide (2003.1026 and 1027); one female with
soft parts dissected in Hydromatrix sealed in a glass
slide (2003.1024); two valves stored in a cavity slide
(2003.1028); seven whole specimens critically point
dried (2003.979, 980, 984–987, 997); three male spec-
imens critically point dried each with one valve
removed (2003.990, 992, 994).

Etymology
Named for Professor Elisabeth Alve (University of
Oslo), friend and collaborator, who while researching
the foraminiferal habitats of the Hamble creeks, in
particular that of the agglutinating species *Balticam-
mina pseudomacrescens* (Bronniman, Lutze & Whit-
taker) – the 'highest' of the high salt marsh
foraminifera – and being of an inquisitive nature,
found a niche that does not appear to have
been searched before . . . and discovered the ostracod
Terrestricythere.

Diagnosis
Species of *Terrestricythere* with five articulated
podomeres in antennula (podomeres four and five
fused) and four articulated podomeres in L7
endopodite. L7 terminating in one long and one short
claw; long claw approximately five times length of
short claw. Each valve bearing laterally three excep-
tionally long sensilla with bifurcated ends. Male cop-
ulatory appendage with two distal processes, larger
elongate, curved, smaller hook-shaped.

Description of adult male (Figs 1–6)
Carapace: Lateral view posterior more rounded than
anterior. Dorsal margin strongly curved, with poste-
rior and anterior angle. Ventral margin gently convex.
LV larger than RV with most overlap dorsally. Dorsal
view ovoid, posterior more rounded than anterior;
LV with small lobe-like extension overlapping RV
towards anterior margin. Hinge 'visordont' (see 'The
hinge of *Terrestricythere*', below, for formal definition),
with two teeth on RV situated towards anterior and
posterior margins and joined by ridge running along
dorsal margin. Lobes interlock and rotate in two pits
on hinge of LV. As carapace opens, dorsal portion of LV
slides over RV (Fig. 3). Calcified inner lamella forms
'U' shape both anteriorly and posteriorly around pits
on LV; calcified inner lamella anteriorly broader than
posteriorly. Adductor muscle scars consisting of five
elongate scars, slightly offset, but parallel with each
other and anteriorly with one rounded scar (Fig. 3).
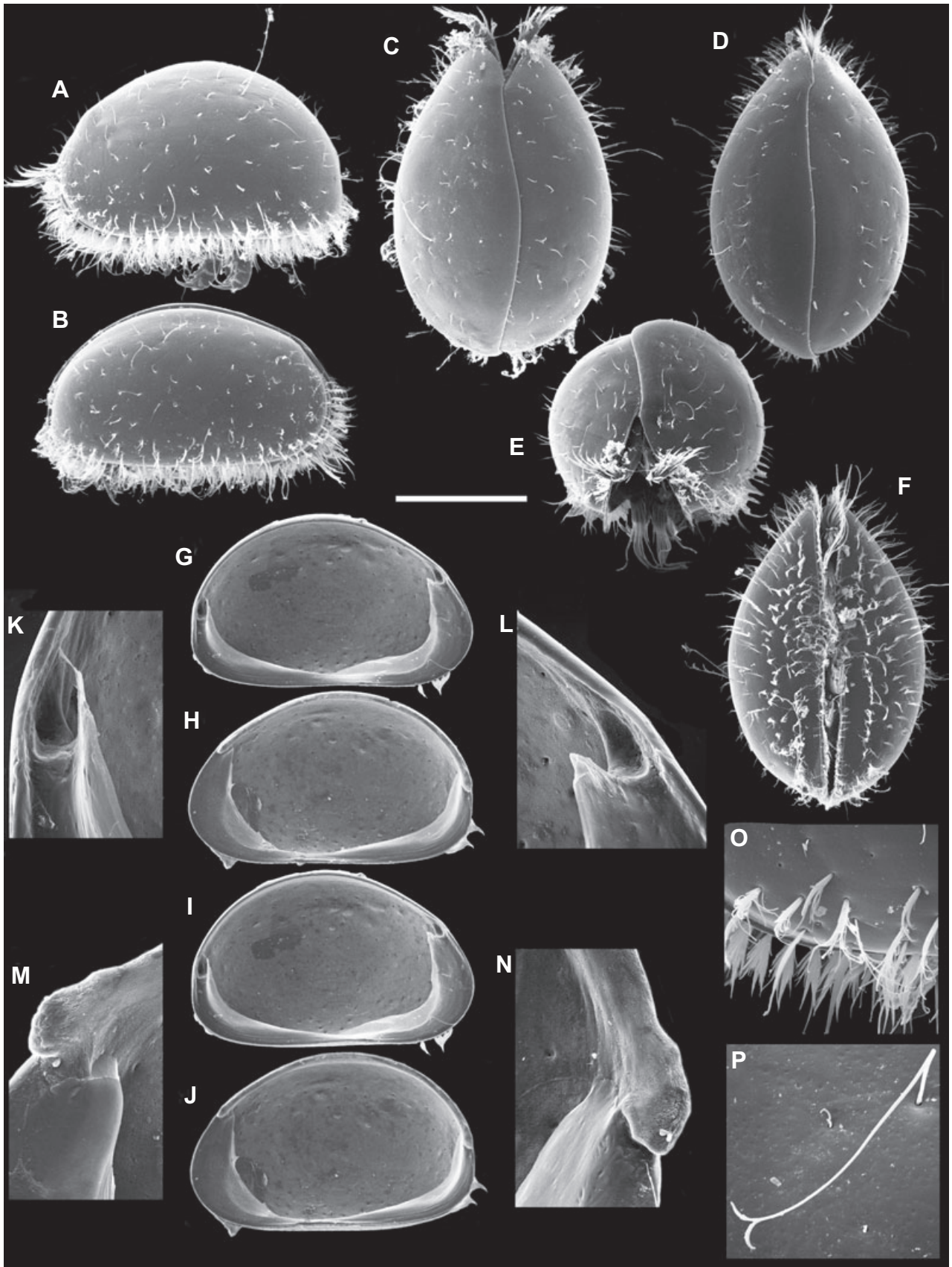Dorsally with six or seven small, round scars near

Figure 1. *Terrestricythere elisabethae* **sp. nov.** A, left lateral view of carapace (2003.979; scale bar = 200 μm). B, right lateral view of carapace (2003.997; scale bar = 200 μm). C, dorsal view of open carapace (2003.980; scale bar = 200 μm). D, dorsal view of closed carapace (2003.986; scale bar = 200 μm). E, anterior view of open carapace (2003.980; scale bar = 200 μm). F, ventral view of carapace (2003.985; scale bar = 200 μm). G & I, stereo pair of internal view of left valve (2003.1028; scale bar = 200 μm). H & J, stereo pair of internal view of right valve (2003.1028; scale bar = 200 μm). K, posterior hinge socket of left valve (2003.1028; scale bar = 45 μm). L, anterior hinge socket of left valve (2003.1028; scale bar = 45 μm). M, anterior hinge lobe of right valve (2003.1028; scale bar = 45 μm). N, posterior hinge lobe of right valve (2003.1028; scale bar = 45 μm). O, ventral sensilla of carapace (2003.987; scale bar = 57 μm). P, long sensillum of carapace (2003.1014; scale bar = 30 μm).

hinge. Surface of valves smooth, but with approximately 142–153 normal pores on each valve, more densely packed towards ventral margin (Fig. 4). Dorsally, sensilla of pore systems simple, but further towards ventral margin sensilla become increasingly bushy. Marginal pore canals numerous with protruding bushy 'shaving brush' sensilla. Each valve with additional three unusually long sensilla (up to 145 μm in length) originating from mid lateral position, often with bifurcating tip.

An1: five segmented, robust and stout (Fig. 5). 1st podomere subquadrate. 2nd podomere subquadrate with one long and one shorter setae on ventral edge, one mid-apical seta and one short subapical-dorsal seta. 3rd podomere subquadrate with four apical setae. 4th podomere elongate, with four setae on dorsal edge and six dorsal-apical setae. 5th podomere with three apical setae and one apical aesthetasc.

An2: robust, stout and biramous (Fig. 5). 1st podomere (coxa) broad, with one anterior-apical and one posterior-apical setae. 2nd podomere (basis) with one small mid-positioned seta, and one longer anterior apical seta. Exopodite protrudes from anterior-apical corner of basis; consists of small rounded plate supporting seven or eight long and one short setae; long setae reach past distal end of limb with short setules along distal half, and terminate in small hooks. Endopodite with three podomeres. 1st podomere with three posterior-proximal aesthetascs, one large and one smaller claw on posterior edge. 2nd podomere elongate with one posterior-subproximal aesthetasc, two claws on posterior edge, one aesthetasc and one claw in posterior-subapical position, two anterior-subapical claws and two anterior-apical claws. 3rd podomere small and subquadrate apically with four claws and one aesthetasc.

Md: coxa small, with reduced outer margin; with one seta on outer edge and five large and two smaller teeth (Fig. 5). Outermost tooth curved with setules, next tooth broad and rounded, with many small setules along edge. Other teeth robust and smooth. Basis with two setae on inner edge and branchial plate (exopodite) on outer edge consisting of one long seta

with flat end. Endopodite consists of three quadrate podomeres. 1st podomere with two setae in inner-proximal position and two inner-apical setulous setae. 2nd podomere with two outer-apical setae and one long, one short setae and one claw on inner-apical corner. 3rd podomere with one long, one mid-length and one short, curved claws. A row of eight closely spaced, setulous rake setae (= filter grille?) arising on palp near basis-endopodite joint; whether these setae inserted on basis or on proximal podomere of endopodite uncertain.

Oesophagus: in living specimens an amber-coloured plate was observed through the carapace, apparently within the oesophagus, in mid-position, anterior of maximum height. In dissections the plate was seen to have numerous setules pointing up towards the stomach.

Mx: endopodite with two segments, 1st podomere with one stout seta on outer edge and with one stout and one smaller setae on outer apical corner (Fig. 5). Final podomere quadrate, with two claws and two setae. 1st, 2nd and 3rd endites with numerous, setulous setae. Large, broad setulous seta originates near base of 2nd endite. Branchial plate with two large, broad, setulous reflexed setae and 18 setulous setae arranged around posterior edge.

L5: four segmented (Fig. 6). Protopodite with exopodite inserted on posterior-distal edge and represented by one long, setulous seta. Apically, protopodite with one long and four shorter setae on inner edge. 1st endopodite podomere elongate with four spines, two setulous setae and numerous setules on anterior edge; 2nd small and rectangular, wider than long; 3rd with one small posterior-apical seta and apically fused with large, broad, proximally curved claw.

L6: five segmented and robust (Fig. 6). Protopodite with exopodite inserted on posterior-distal edge and consisting of one long, setulous seta. Additionally with one seta on anterior edge and apically with three setae on anterior corner. 1st endopodite podomere elongate with numerous setules along anterior edge and with two large and two small claws on anterior-apical cor-
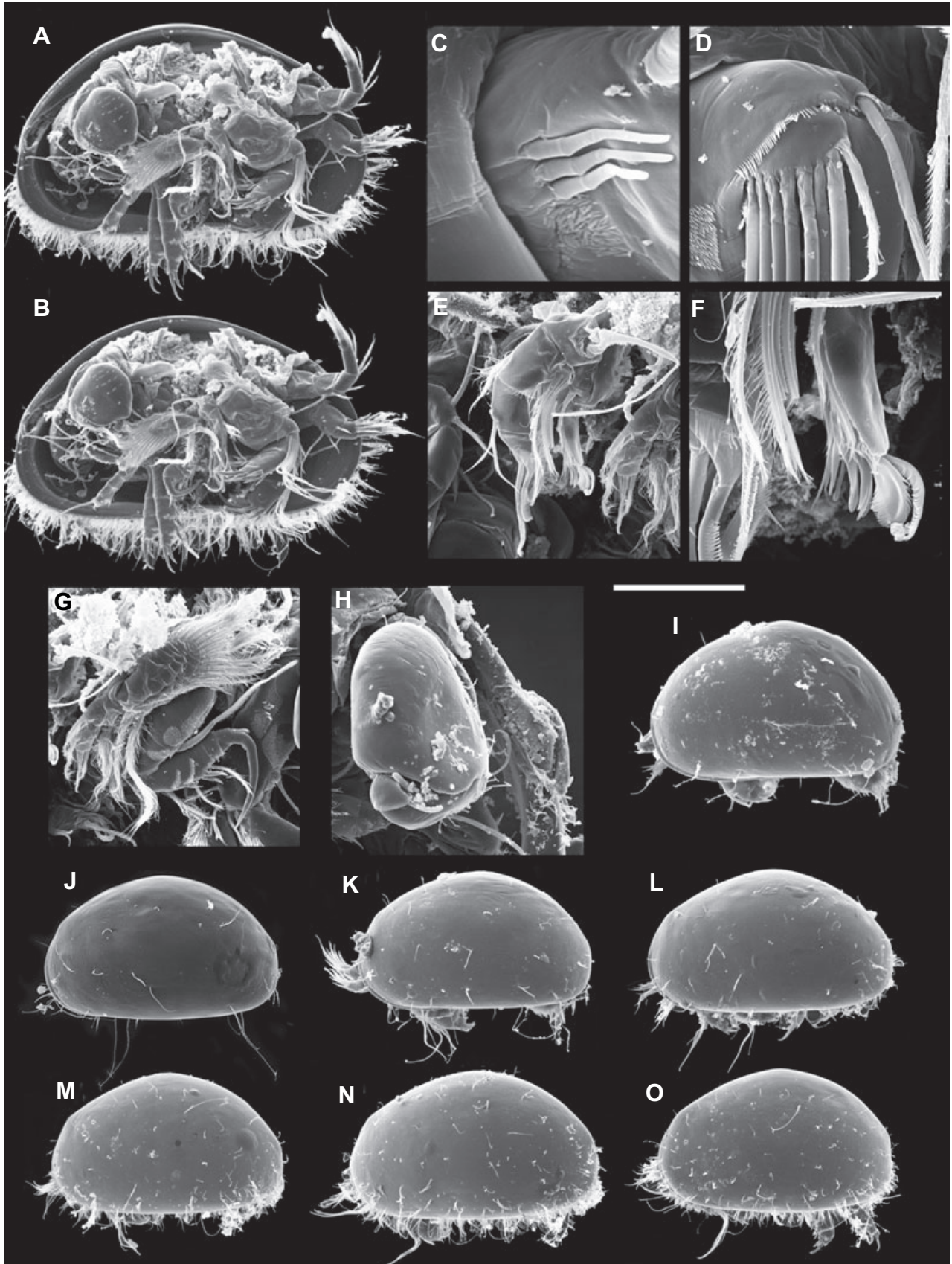
Figure 2. *Terrestricythere elisabethae* **sp. nov.** A & B, stereo pair of male with right valve removed (2003.994; scale bar = 167 μm). C, aesthetascs of 1st endopodite podomere of antenna (2003.984; scale bar = 13 μm). D, exopodite plate of antenna (2003.994; scale bar = 23 μm). E, mandible (2003.992; scale bar = 65 μm). F, mandibular coxa and rake setae (2003.992; scale bar = 21 μm). G, maxillula and fifth limb of male (2003.992; scale bar = 90 μm). H, hemipene of male (2003.990; scale bar = 57 μm). I, left lateral view of carapace of A-7 instar (2003.1000; scale bar = 75 μm). J, left lateral view of carapace of A-6 instar (2003.1017; scale bar = 93 μm). K, left lateral view of carapace of A-5 instar (2003.1001; scale bar = 108 μm). L, left lateral view of carapace of A-4 instar (2003.1003; scale bar = 125 μm). M , left lateral view of carapace of A-3 instar (2003.1008; scale bar = 150 μm). N, left lateral view of carapace of A-2 instar (2003.1010; scale bar = 170 μm). O, left lateral view of carapace of A-1 instar (2003.1014; scale bar = 208 μm).
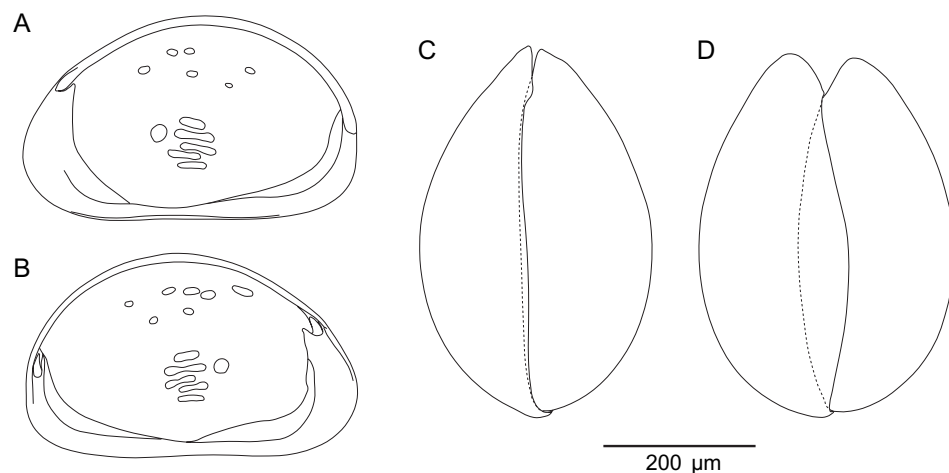

Figure 3. *Terrestricythere elisabethae* **sp. nov.** 'Visordont' hinge and muscle-scars. A, internal view of right valve. B, internal view of left valve. C, dorsal view of whole, closed carapace. D, dorsal view of whole, open carapace showing the larger left valve overriding the right valve dorsally. Dotted line indicates valve overlap.
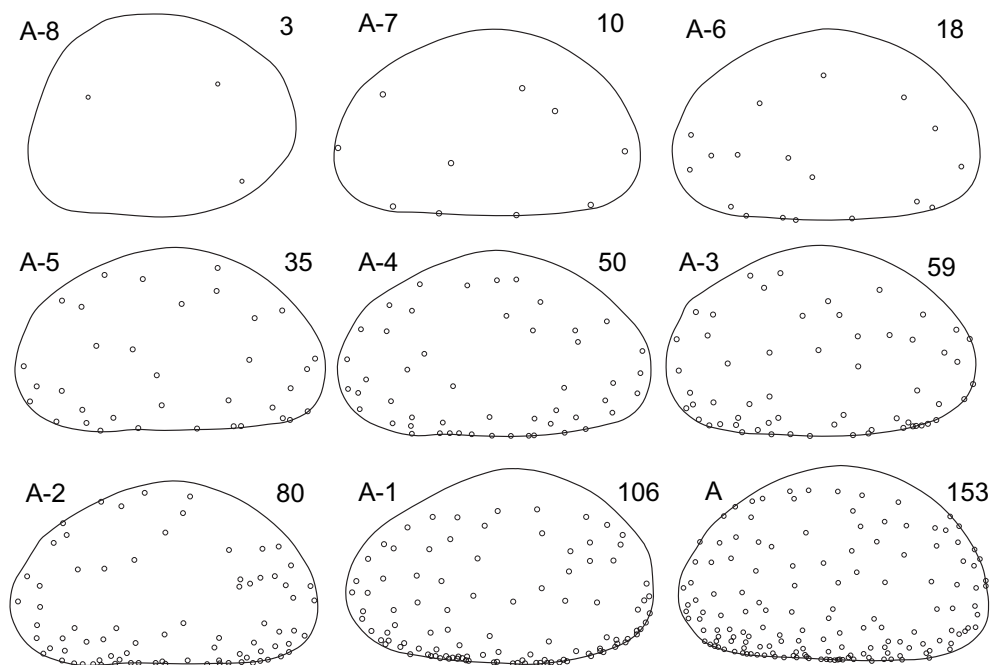

Figure 4. *Terrestricythere elisabethae* **sp. nov.** Maximum number and position of pore systems on left valves of instars.
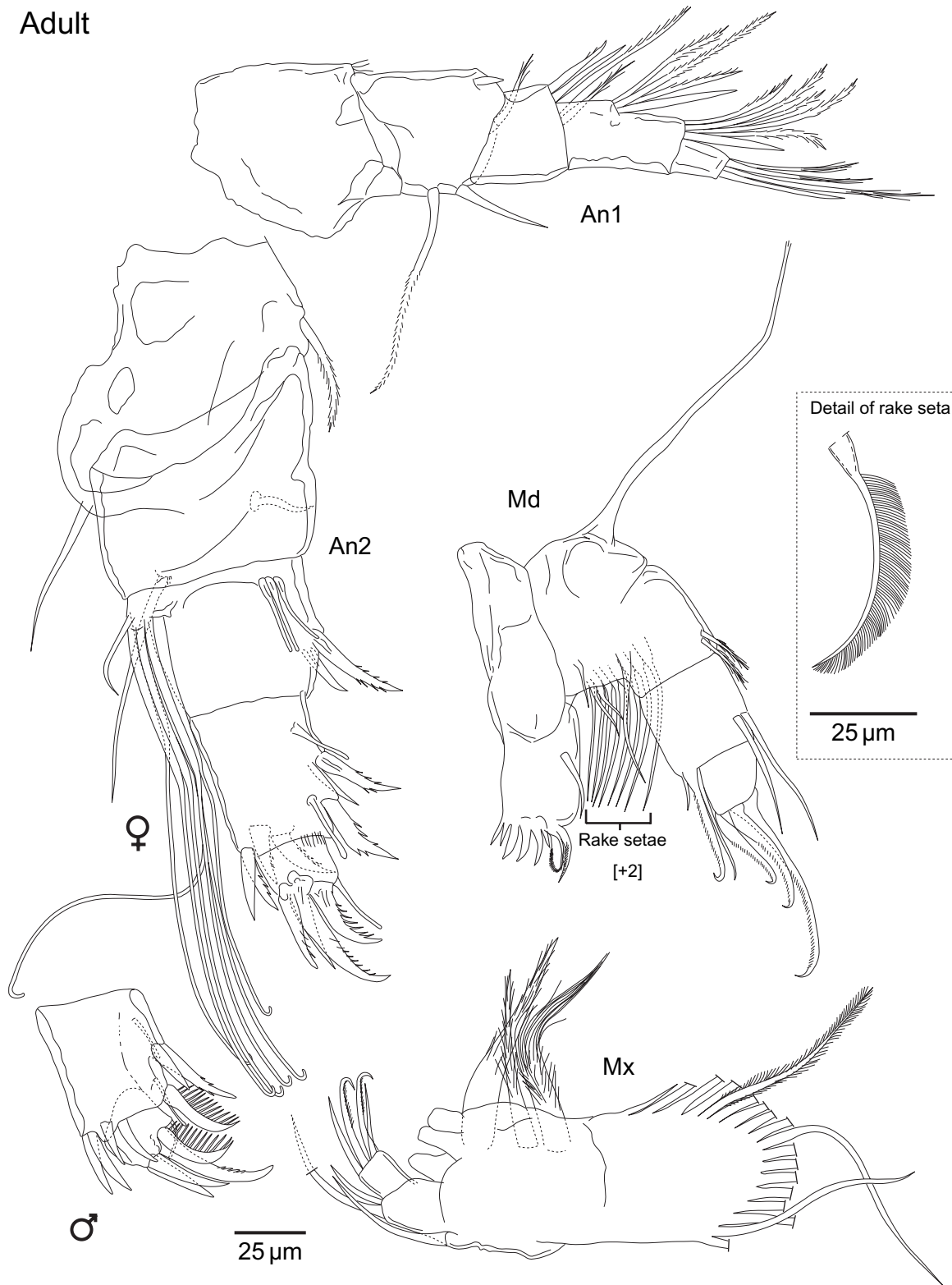
Adult

Figure 5. *Terrestricythere elisabethae* **sp. nov.** Adult instar. An1 (2003.1024 female), An2 (2003.1023 female, 2003.1025 male), Md (2003.1024 female), detail of rake seta (2003.1027 male), Mx (2003.1025 male).
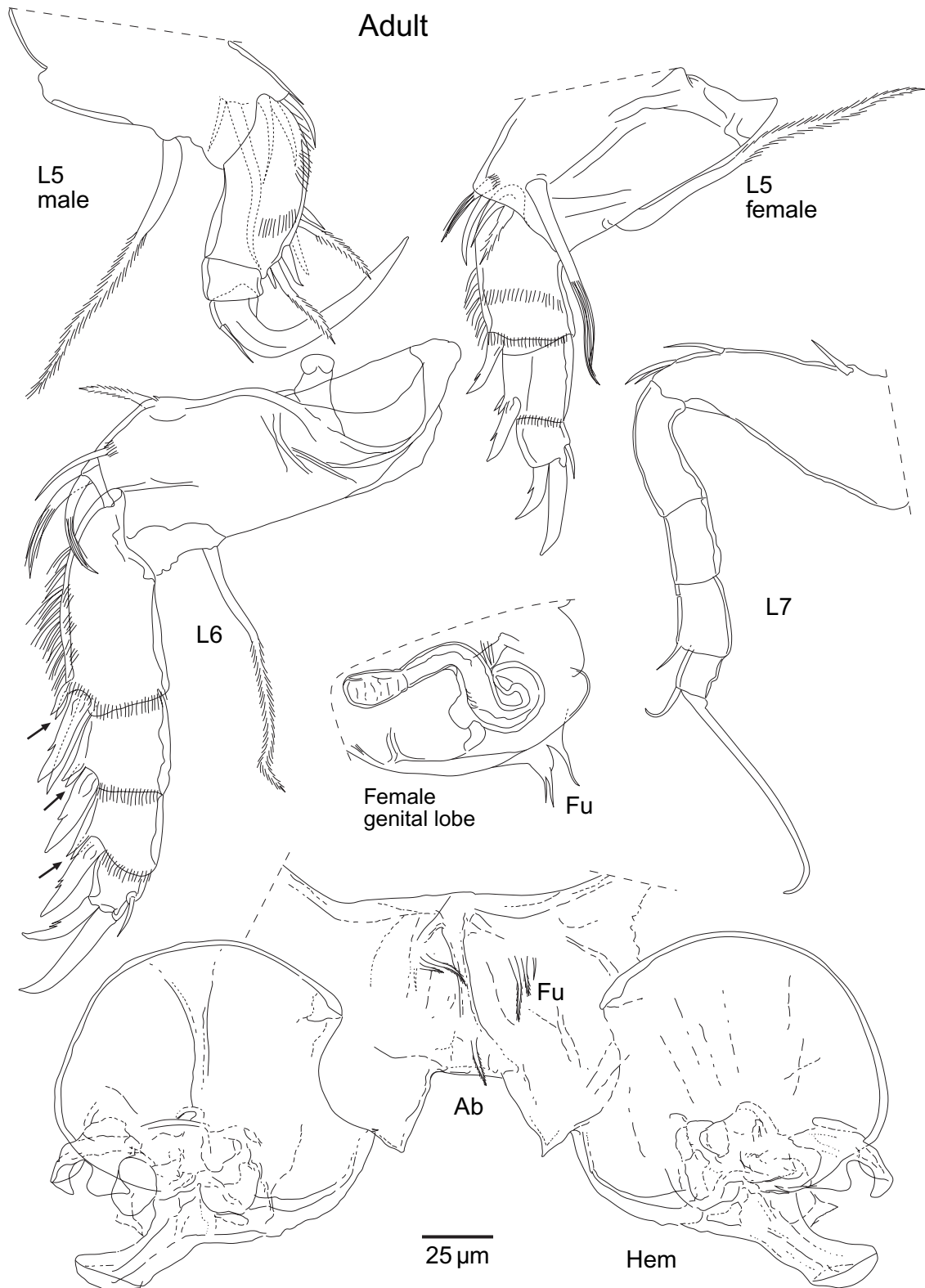
Figure 6. *Terrestricythere elisabethae* **sp. nov.** Adult instar. L5 (2003.1026 male), L5 (2003.1024 female), L6 (2003.1025 male), L7 (2003.1025 male), female genital lobe (2003.1023 female), Hem (2003.1025 male).

ner. 2nd and 3rd endopodite podomeres both quadrate and each with one large and two small claws on anterior-apical corner. 4th endopodite podomere subquadrate with one small seta on posterior edge and apically with one large, and one smaller claw.

L7: five segmented and slender (Fig. 6). Protopodite proximally broad with two setae on anterior edge, and two anterior-subapical setae; exopodite seta (posterior-proximal) apparently absent. 1st endopodite podomere proximally curve; 2nd without setae; 3rd with one small anterior-apical seta; 4th with one short, curved, smooth claw and one much longer smooth, curved claw.

Fu: reduced to pair of small protuberances each bearing three small setulous setae, situated between bases of Hem (Fig. 6).

Hem: rounded with triangular process at base (Fig. 6). Distally with two clasping processes. Smaller clasping process with hooked end, blunt process on inner edge and rounded lobe on outer edge. Larger clasping process elongate with convexly curved edges, inner edge more curved than outer edge, and with rounded end.

Description of adult female

Carapace, An1, An2, Md, Mx, L6 and L7 similar to those of adult male.

L5: four segmented (Fig. 6). Protopodite with exopodite inserted on posterior-distal edge and consisting of one long, setulous seta. Apically, protopodite with one long and four shorter setae on inner edge. 1st endopodite podomere with one anterior-apical seta and numerous setules along anterior edge; 2nd with one large claw and two small spines on anterior-apical corner; 3rd subquadrate with one small seta on posterior edge and apically with one large, and one smaller claw.

Fu: pair of small protuberances each bearing three short distal setae, situated between genital lobes.

Female genitals: rounded lobe with wide internal duct (Fig. 6). Duct coiled at anterior end and straight posteriorly, terminating in rounded end.

Remarks

In addition to *T. elisabethae* sp. nov. there are two other described species belonging to the genus *Terrestricythere*: *T. ivanovae* Schornikov, 1969 and *T. pratensis* Schornikov, 1980. The carapace shape of *T. elisabethae* is most similar to that of *T. pratensis*, although our species is slightly higher in lateral view. In contrast, *T. ivanovae* is distinctly more elongate than *T. elisabethae* and *T. pratensis*. The three long,

lateral sensilla on each valve in *T. pratensis* and *T. elisabethae* seem to be absent in *T. ivanovae*. The An1 of *T. ivanovae* has six articulated podomeres, compared with five in both *T. pratensis* and *T. elisabethae*.

In other podocopid ostracod families the number of articulated podomeres is regarded as significant at generic level, e.g. in the Loxoconchidae (see Athersuch & Horne, 1984), but we do not think it would serve any useful purpose at present to split the genus *Terrestricythere* on the basis of this character. Both *T. ivanovae* and *T. pratensis* have an L7 that terminates with a long claw and a shorter claw approximately half the length of the long claw (Fig. 7). In *T. elisabethae* the shorter claw of the L7 is only about 1/5th of the length of the long claw. Also the L7 endopodite of *T. ivanovae* has only three articulated podomeres (the distal two being fused), while *T. elisabethae* and *T. pratensis* have four.

The hemipenes of all three species consist of a rounded basal capsule with two distal processes (Fig. 7). The outer edge of the larger process is smoothly curved in both in *T. ivanovae* and *T. elisabethae*, but in *T. pratensis* it is broader than in the other two species and bears an anvil-shaped protuberance on its outer edge which is pointed at both ends. The smaller process is short and rather quadrate in *T. ivanovae*, narrow and curved in *T. pratensis*, and rather broad and distinctly hook-shaped in *T. elisabethae*.

Schornikov's (1969) original illustration of the L7 of *T. ivanovae* was misinterpreted by Horne, Cohen & Martens (2002: 33) who included the incorrect statement . . . 'Seventh limb bearing a branchial plate with three rays' . . . in their diagnosis of the Terrestricytheroidea; the apparent branchial plate is in fact the furca.
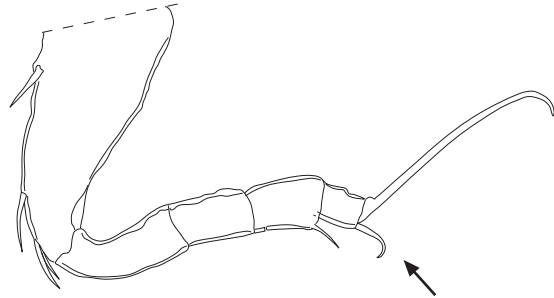
Ontogeny

The following section does not provide a detailed description of each instar, but notes the changes from one instar to the next.
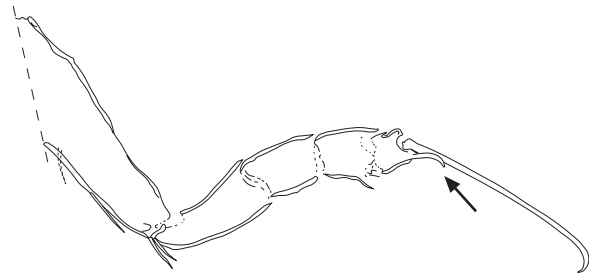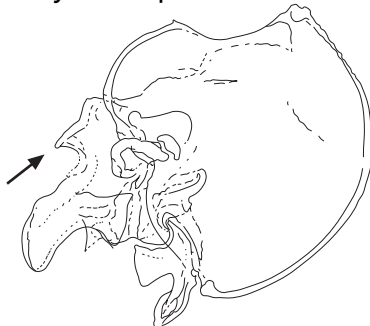
Instar A-8

Carapace: Length 130 μm, height 90 μm (one specimen measured). Uncalcified and flexible, rounded, smooth surface. Dorsal margin strongly curved, ventral margin gently curved. Hinge adont. Each valve with three pore systems (Fig. 4).

An1: five podomeres, last four all wider than long (Fig. 8). 3rd podomere with one rounded, broad, dorsal-apical seta; 4th with two broad, short, rounded apical setae; 5th with four short, broad, rounded, apical setae.
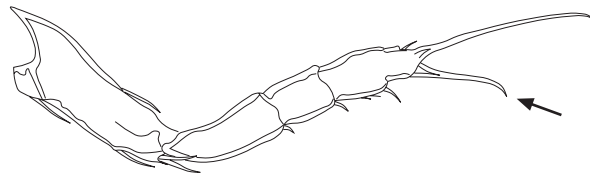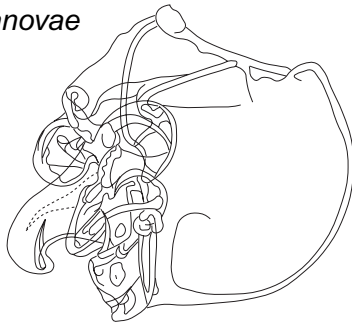
T. elisabethae sp. nov.

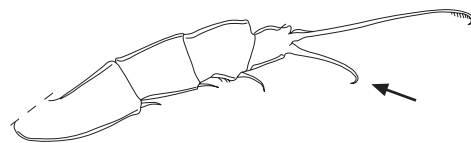*Terrestricythere* sp.

T. ivanovae

T. pratensis

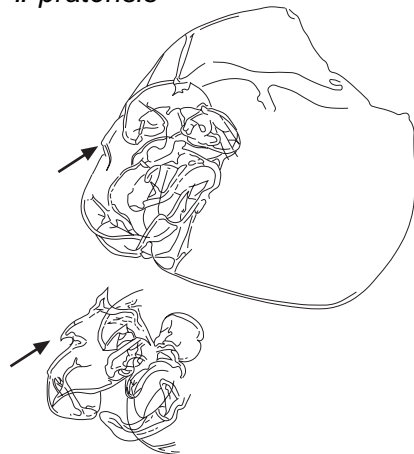**Figure 7.** Pictorial key of the known species of *Terrestricythere*. Comparative illustrations of hemipenes and L7. *T. ivanovae* and *T. pratensis* drawn after Schornikov (1969, 1980) respectively.
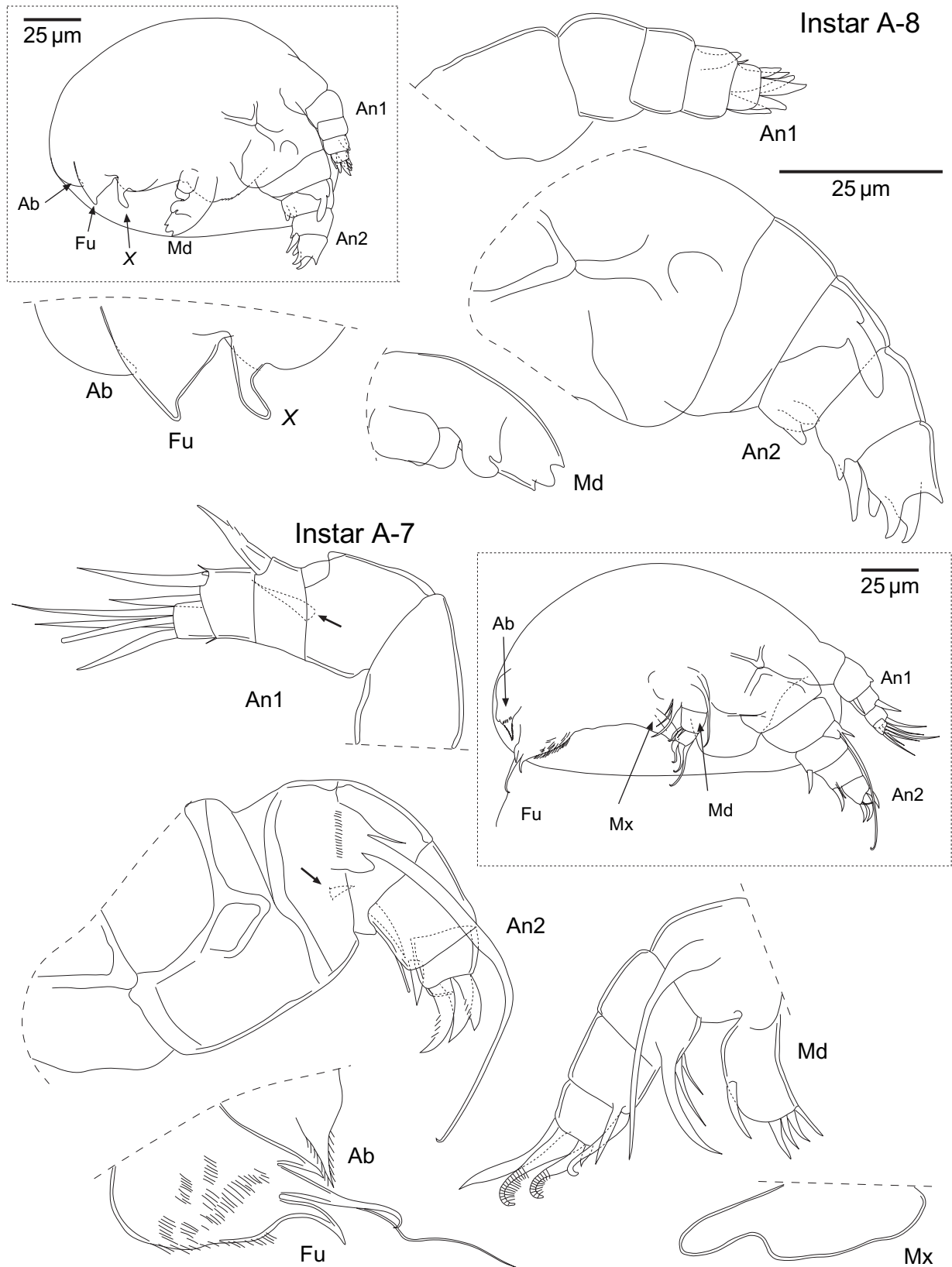
Figure 8. *Terrestricythere elisabethae* **sp. nov.** A-8 instar (2003.1029). A-7 instar; reconstruction of body plan based on 2003.1033. An1 (2003.1032), An2 (2003.1030), Md (2003.1030), Mx (2003.1030), Fu (2003.1031).

An2: five podomeres, coxa large and broad (Fig. 8). Basis wider than long. Exopodite plate with one broad, rounded, short seta. 1st endopodite podomere with two short, lobe-like setae on posterior edge; 2nd with one short and one longer lobe-like posterior-apical setae. Final podomere with four rounded, lobe-like setae, two larger of which are hooked.

Md: segmentation indistinct (Fig. 8). Lobe on inner edge incipient coxa (?). Palp with two lobes on inner edge and terminates with three small lobes.

Lobe X: lobe anterior to Fu; elongate and hook shaped (Fig. 8).

Fu: rami triangular in shape, broad base, slightly curved distally (Fig. 8).

Ab: lobe at posterior of body, with rounded end (Fig. 8).

Instar A-7
Carapace: length 152–160 µm, height 96–100 µm. Calcified (Fig. 2). Lateral view rounded, with LV overlapping RV. Anterior slightly more rounded than posterior. Maximum height approximately at mid-length. Dorsal margin strongly curved, ventral margin straight. RV with list. Carapace surface smooth. Each valve with nine pore systems (Fig. 4).

An1: all setae more robust, and longer than in previous instar (Fig. 8). 2nd podomere with additional apical seta. 5th podomere with three apical setae and one apical aesthetasc.

An2: exopodite now with one long seta with hooked end, one short seta and one small lobe (Fig. 8). Basis with additional one small mid-positioned seta. 2nd endopodite podomere with one posterior-apical claw and one aesthetasc. Final podomere with three stout claws and one bent aesthetasc.

Md: coxa with four teeth and one subapical seta on outer edge (Fig. 8). Exopodite consisting of one long seta. 1st endopodite podomere with three apical setae on inner corner; 2nd with one apical claw and one apical seta on inner corner; 3rd with three claws.

Mx: Anlage consisting of rounded lobe, directly behind Md (Fig. 8).

Fu: rami short, stout and rounded, with many setules on posterior edge (Fig. 8), terminating with two short, stout claws and one long claw with thin seta protruding from distal half; seta longer than claw.

Ab: directly posterior of Fu, consisting of stout setulous end (Fig. 8).

Instar A-6
Carapace: length 170–190 µm, height 105–130 µm. Carapace shape similar to that of previous instar (Fig. 2). Each valve with 18 pore systems (Fig. 4).

An1: 2nd podomere with additional small, stout seta on dorsal-apical corner (Fig. 9). 4th podomere with additional apical claw and seta.

An2: coxa with additional seta on posterior edge (Fig. 9). Exopodite with one additional long, hooked seta. 1st endopodite podomere with two additional aesthetascs on posterior edge; 2nd with one additional claw on anterior-apical corner.

Md: coxa with additional tooth (Fig. 9). 2nd endopodite podomere with additional seta on outer-apical corner.

Mx: transformed from *Anlage* to feeding appendage; palp simple, not segmented, terminating in one stout, curved claw (Fig. 9). 3rd endite terminates with one stout seta, 2nd with three, 1st with two. Branchial plate formed (number of setae unknown as folded in all specimens).

Fu: each ramus with additional long claw, similar to pre-existing long claw, with thin seta protruding from distal half (Fig. 9).

Instar A-5
Carapace: length 205–220 µm, height 128–144 µm. Overall shape similar to previous instar (Fig. 2). Each valve with 35 pore systems (Fig. 4).

An1: similar to that of previous instar (Fig. 10).

An2: 1st endopodite podomere with one additional aesthetasc, now forming group of three (Fig. 10). Exopodite with additional long, hooked seta, forming group of three long setae, one short seta and one small lobe.

Md: additional seta protruding from inner edge of basis (Fig. 10).

Mx: endopodite segmented; 1st podomere with one stout, curved seta on apical-outer edge (Fig. 10). 2nd podomere with additional stout apical seta, forming group of two. Endites with numerous apical setae (number unknown).

L5: Anlage; rounded elongate lobe, tapering distally to point (Fig. 10).

Fu: similar to that of previous instar (Fig. 10).

Instar A-4
Carapace: length 235–260 µm, height 152–163 µm. Overall shape similar to previous instar (Fig. 2). Each valve with 47–50 pore systems (Fig. 4).

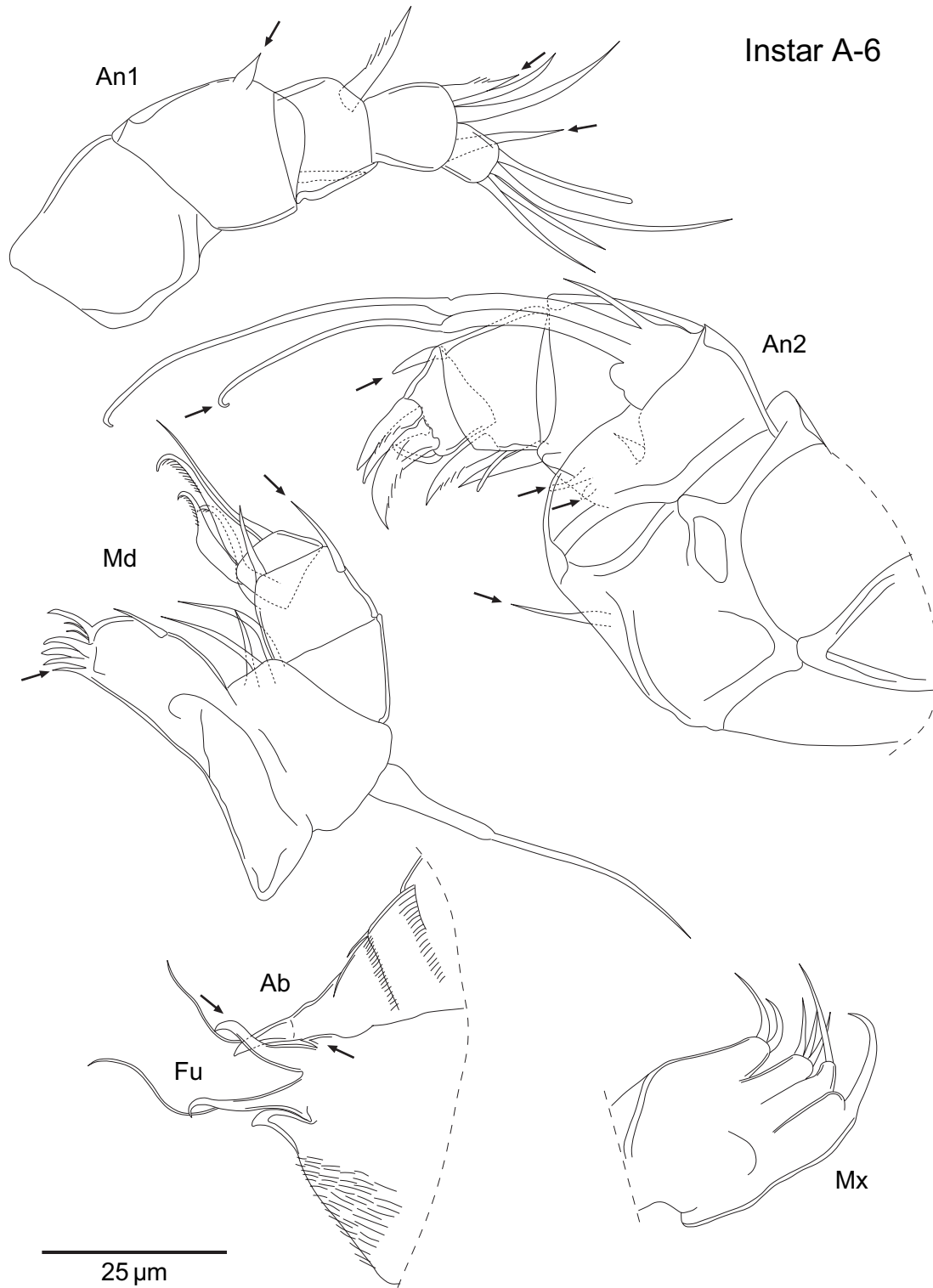**Figure 9.** *Terrestricythere elisabethae* **sp. nov**. A-6 instar (2003.1034).
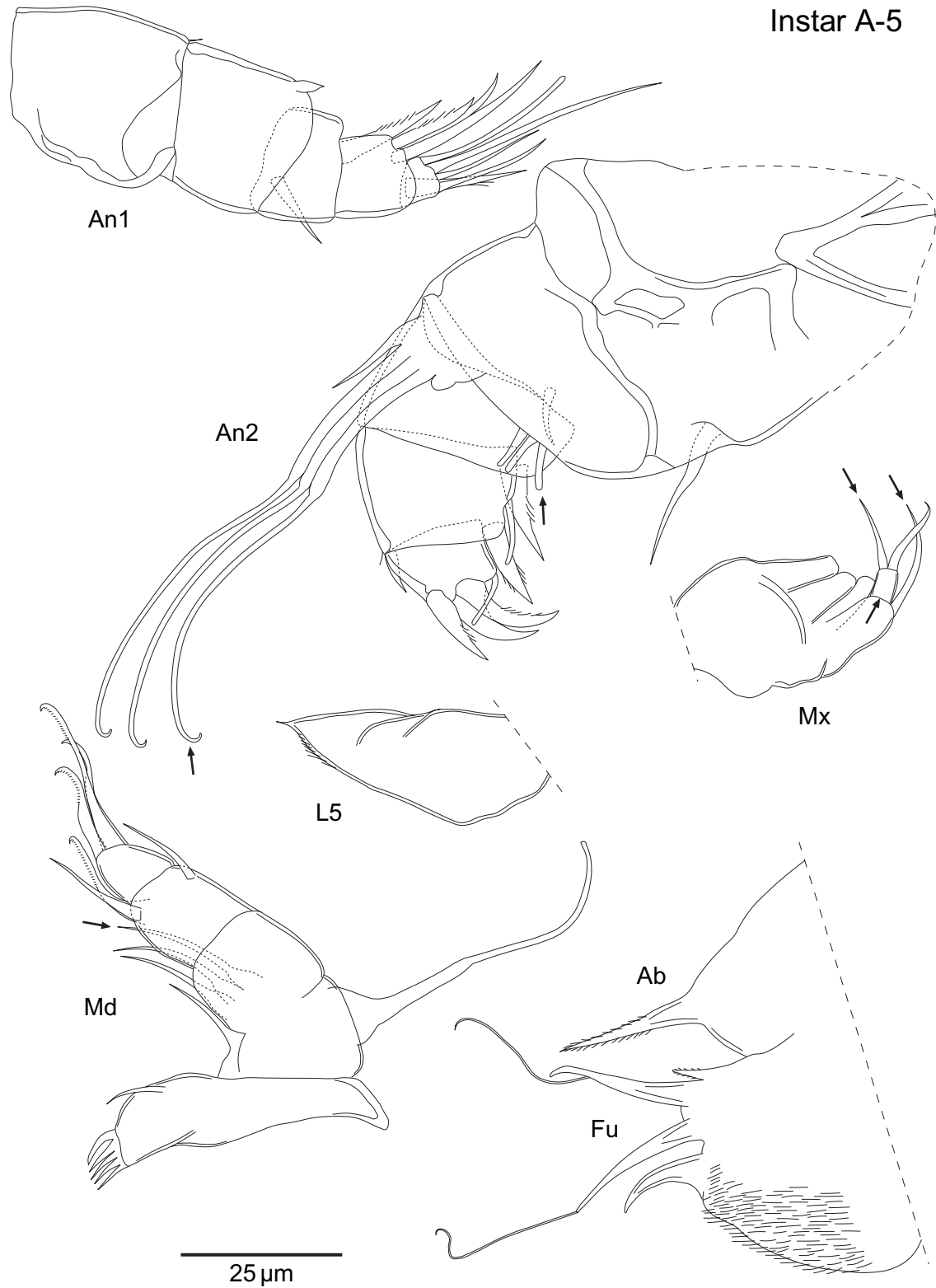
Instar A-5

Figure 10. *Terrestricythere* **elisabethae sp. nov.** A-5 instar. An1 (2003.1035), An2 (2003.1035), Md (2003.1037), Mx (2003.1037), L5 (2003.1037), Fu (2003.1036).

An1: 2nd podomere with additional long seta on ventral edge; 4th with additional apical short seta, forming group of five (Fig. 11).

An2: coxa with additional seta on anterior edge (Fig. 11). Exopodite with four long setae. 2nd endopodite podomere with new aesthetasc on posterior edge and small claw on anterior-apical corner; 3rd with four stout claws.

Md: endopodite with two new setae on inner edge (Fig. 11).

Mx: endopodite with one new apical seta on 1st podomere and new apical seta on final podomere. Additional large, broad, setulous seta near base of 2nd endite (Fig. 11).

L5: transformed from *Anlage*; four podomeres, 1st podomere (protopodite) robust and broad, tapering distally, with three small, stout, anterior-apical claws and long seta (exopodite) on posterior edge. 2nd podomere elongate; 3rd quadrate with small anterior-apical spine; 4th trapezoid with one small seta on posterior edge, one small apical claw and one long apical claw (Fig. 11).

L6: Anlage; rounded elongate lobe, tapering distally to point (Fig. 11).

Fu: each ramus reduced to two small spines and one long claw (Fig. 11).

Instar A-3
Carapace: length 287–300 µm, height 178–185 µm. Overall shape similar to previous instar (Fig. 2). Each valve with 55–59 pore systems (Fig. 4).

An1: 2nd podomere with extra seta on ventral edge next to existing long seta (Fig. 12). 4th podomere with two new setae at mid-point of dorsal edge.

An2: basis with additional seta on anterior-apical corner (Fig. 12). Exopodite with one new, long, seta producing group of five long and one short setae. 2nd endopodite podomere with additional, small, stout claw on posterior edge and small stout claw on anterior-apical corner.

Md: endopodite with extra seta on outer-apical corner of 2nd podomere (Fig. 12).

Mx: endopodite with new seta on outer edge of 1st podomere (Fig. 12).

L5: 3rd podomere with additional small spine on anterior-apical corner (Fig. 13).

L6: transformed from *Anlage* (Fig. 13). 1st podomere large and robust with one seta on anterior-apical cor-

ner; 2nd elongate; 3rd elongate with small, stout claw on anterior-apical corner; 4th small and trapezoid, with small seta on posterior edge and one long claw and one shorter claw apically.

L7: Anlage; rounded elongate lobe, tapering distally to point (Fig. 13).

Fu: Each ramus reduced further to two small, setulous claws (Fig. 13).

Instar A-2
Carapace: length 343–360 µm, height 218–230 µm. Overall shape similar to previous instar (Fig. 2). Each valve with 71–80 pore systems (Fig. 4).

An1: 3rd podomere with additional apical seta; 4th with extra seta along dorsal edge and additional seta on ventral-apical corner (Fig. 14).

An2: exopodite with additional long seta (Fig. 14).

Md: basis with two extra setae on inner edge (Fig. 14). 1st endopodite podomere with one additional seta on inner edge and two new setae on outer edge.

Mx: 1st endopodite podomere with extra seta on outer-apical edge (Fig. 15).

L5: protopodite with additional stout seta on anterior-apical corner and additional long, subapical seta (Fig. 15).

L6: now with five podomeres as result of 3rd podomere in previous instar dividing into two (Fig. 15). Protopodite with additional long seta (exopodite) on posterior edge. 2nd podomere with new spine on anterior-apical corner. 3rd podomere wider than long and with robust spine on anterior-apical corner. 4th podomere wider than long and with robust spine and three smaller spines on anterior-apical corner. Final podomere similar to that of final podomere in previous instar.

L7: Transformed into appendage with four podomeres (Fig. 15). 1st podomere elongate, with two small, stout, anterior-apical setae; 2nd and 3rd elongate; 4th small, trapezoid, with one short, curved claw and one long, curved claw.

Fu: Similar to previous instar (Fig. 15).

Instar A-1
Carapace: Length 413–426 µm, height 265–265 µm. Overall shape similar to previous instar (Fig. 2). Each valve with 99–106 pore systems (Fig. 4).

An1: 3rd podomere with two additional, stout apical setae, producing group of four; 4th with one extra,
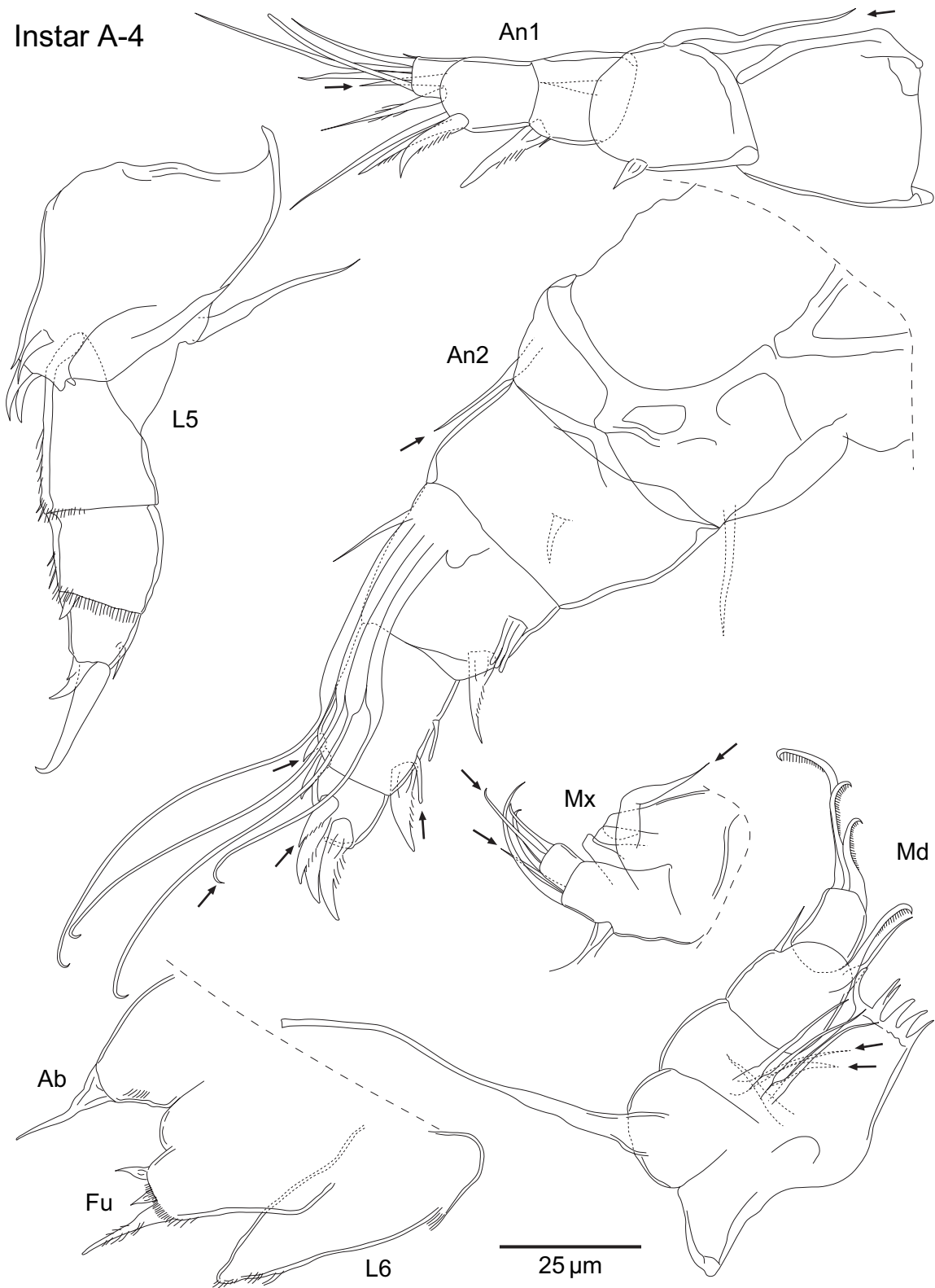
Figure 11. *Terrestricythere* **elisabethae sp. nov.** A-4 instar. An1 (2003.1039), An2 (2003.1039), Md (2003.1039), Mx (2003.1038), L5(2003.1039), L6 (2003.1038), Fu (2003.1038).
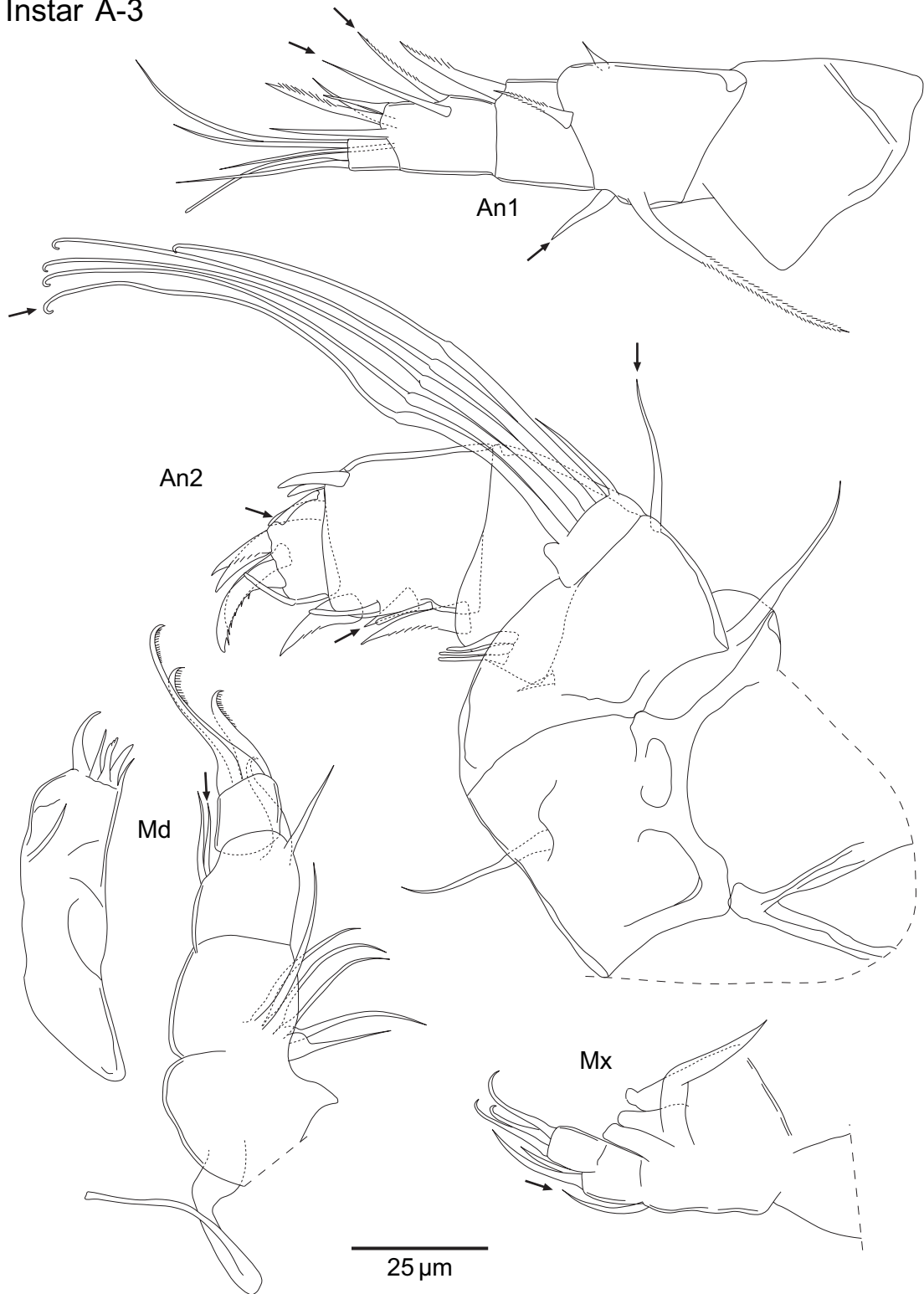
Instar A-3

Figure 12. *Terrestricythere elisabethae* **sp. nov.** A-3 instar. An1 (2003.1042), An2 (2003.1043), Md (2003.1044), Mx (2003.1044).
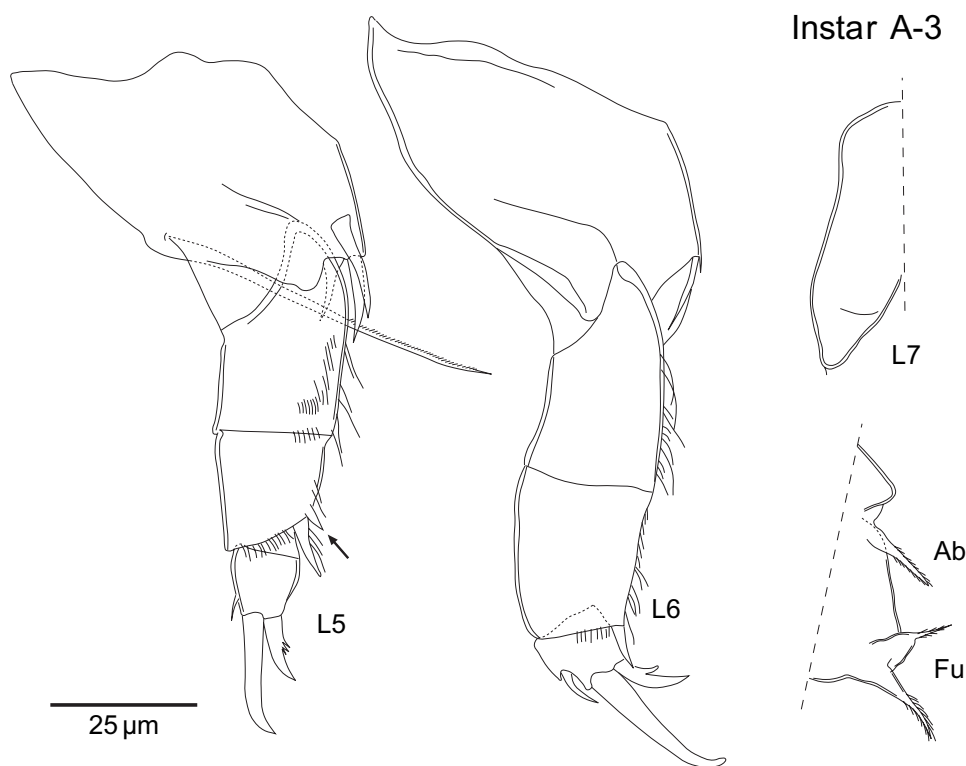
Figure 13. *Terrestricythere elisabethae* **sp. nov.** A-3 instar. L5 (2003.1042), L6 (2003.1040), L7 (2003.1041), Fu (2003.1041).

stout setae in mid-length position producing group of four (Fig. 16).

An2: Exopodite with additional long seta, producing group of seven long and one short setae. 1st endopodite podomere with one new, small claw on posterior-apical corner; 2nd with one additional claw on posterior edge and one new anterior-apical claw (Fig. 16).

Md: 2nd podomere of endopodite with additional small, apical seta on inner edge (Fig. 16).

Mx: similar to that of previous instar (Fig. 16).

L5: 3rd podomere with additional small, anterior-apical spine (Fig. 17).

L6: 1st podomere with two additional setae on anterior edge, and one new anterior-apical seta (Fig. 17).

L7: now with five podomeres with 3rd podomere in previous instar dividing. 1st podomere with additional small seta on anterior edge (Fig. 17).

Fu: similar to that of previous instar (Fig. 17).

Instar adult
Carapace: length 480–500 μm, height 322–340 μm.

Dorsal margin slightly more inflated than in previous instar. Each valve with 142–153 pore systems (Fig. 4).

An1, An2, Md and Mx: similar to that of previous instar (Fig. 5).

L5: male L5 with two long and three short stout setae on anterior edge (Fig. 6). 4th podomere used with large terminal hook. Female L5 similar to that of previous instar (Fig. 6).

L6: 2nd, 3rd and 4th podomeres each with one additional small, anterior-apical spine (Fig. 6).

L7: more elongate than in previous instar (Fig. 6).

Fu: in males fused with base of hemipenes (Fig. 6). Similar to previous instar in females (Fig. 6).

Hem: fully developed (Fig. 6).

Remarks on ontogeny
The appearance of limbs through ontogeny of *Terrestricythere elisabethae* sp. nov. is generally similar to that of other podocopid superfamilies, such as the Cypridoidea, Cytheroidea and Bairdioidea (Fig. 20). The first instar (A-8) of the Cypridoidea, Cytheroidea and Terrestricytheroidea consists of the antennulae, antennae and the *Anlagen* of the mandibles (Fig. 21)
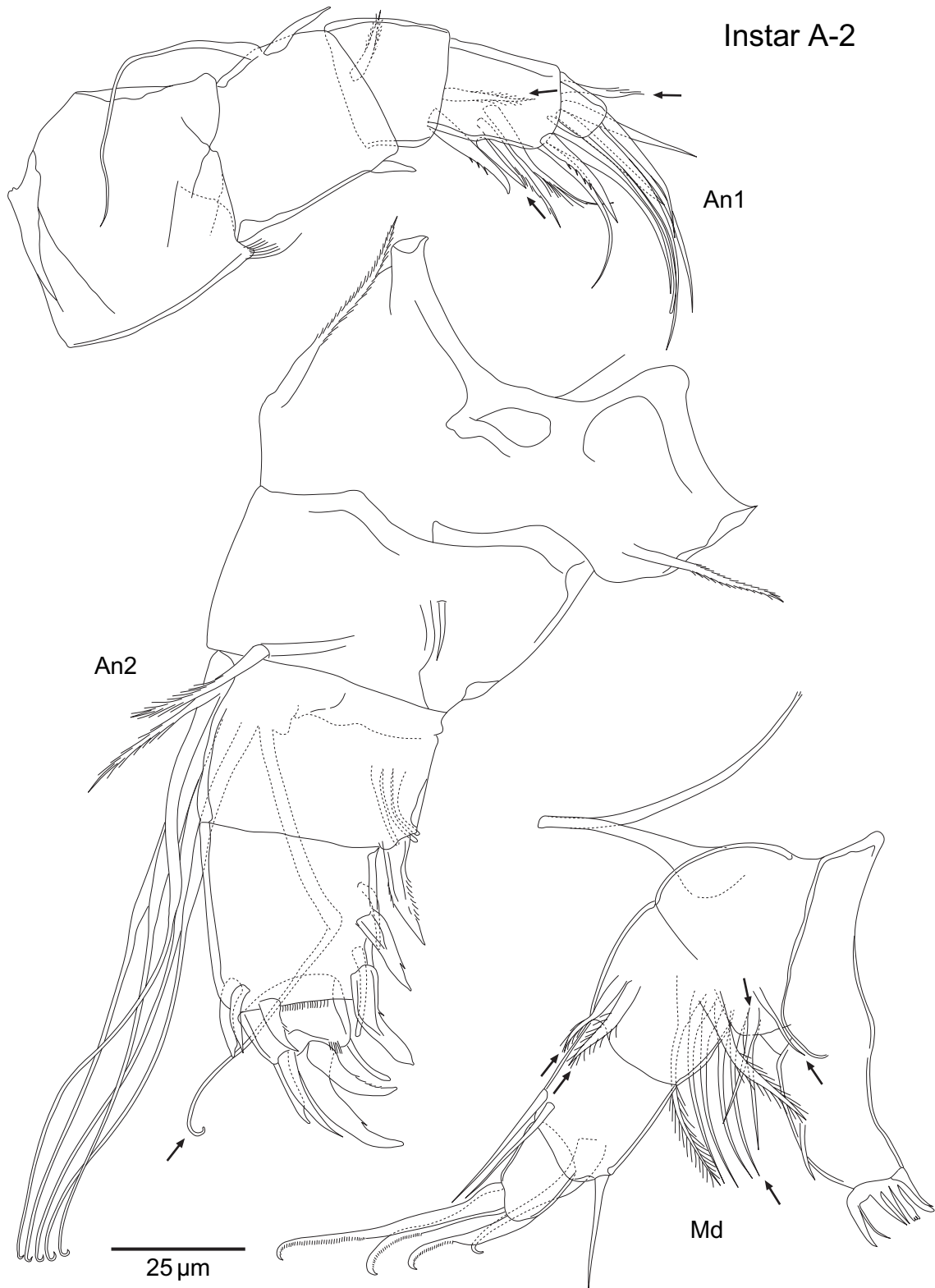
Figure 14. *Terrestricythere elisabethae* **sp. nov.** A-2 instar. An1 (2003.1045), An2 (2003.1045), Md (2003.1046).

Instar A-2

Mx

L5

L7

L6

Ab

Fu

25 μm

Figure 15. *Terrestricythere elisabethae* **sp. nov.** A-2 instar. Mx (2003.1046), L5 (2003.1047), L6(2003.1045), L7(2003.1046), Fu (2003.1046).

(the A-8 instar of the Bairdioidea is unknown; Smith & Kamiya, 2002). The Cytheroidea and Terrestricytheroidea also have the *Anlage* of the furca in this instar, which is missing in the Cypridoidea.

In *T. elisabethae* there is an additional elongate, hooked lobe (labelled *X* in Fig. 8) just anterior of the furca, which is not present in other groups in this instar. These lobes are only present in the first instar and their homology is not clear; their position suggests that they are not the *Anlagen* of the maxillula (the next limb to appear, positioned directly behind the mandible), but if they are *Anlagen* of a pair of thoracic appendages, which are not expressed in later instars, then they are appearing out of sequence. Such a sce-

Figure 16. *Terrestricythere elisabethae* **sp. nov.** A-1 instar. An1 (2003.1048), An2 (2003.1048), Md (2003.1048), Mx (2003.1048).

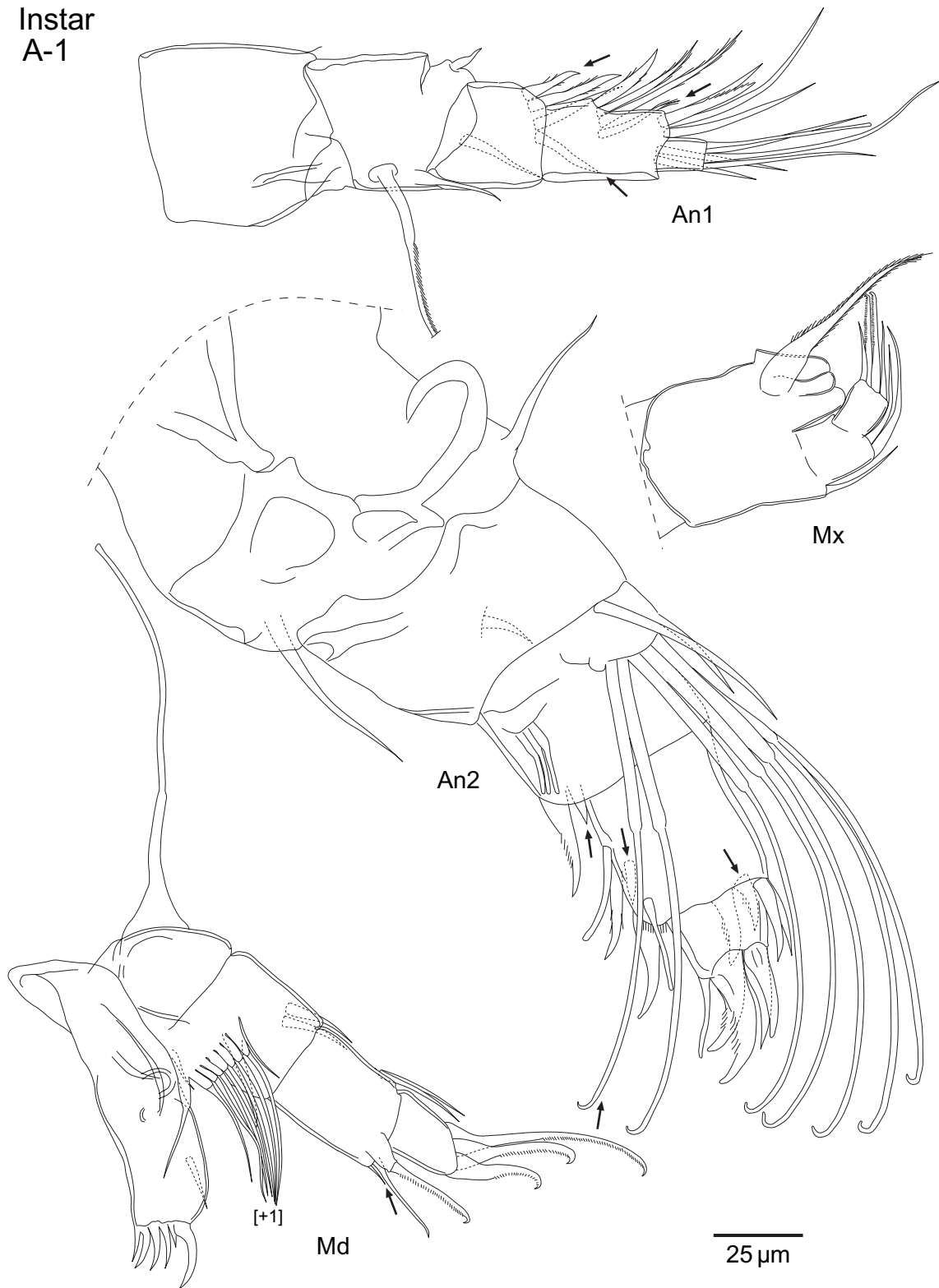**Figure 17.** *Terrestricythere elisabethae* **sp. nov.** A-1 instar. L5 (2003.1048), L6(2003.1048), L7(2003.1048), Fu (2003.1048).

nario of three functional head appendages and a thoracic appendage is in conflict with the accepted idea that a crustacean nauplius has only three pairs of functional head appendages, and sometimes a furca or *Anlagen* of the maxillula (e.g. Dahms, 2000). It would imply that the terrestricytheroidean A-8 instar (and maybe those of other ostracod groups) is not a true nauplius but rather a more advanced stage.

From instar A-7 onwards the ontogenetic appearance of limbs is similar to that of other groups (Fig. 20). The exopodite of the antenna gains an addi-tional long, hooked setae from instar A-7 (one long seta) to instar A-1 (seven long setae); the exopodite of the adult antenna only gains an additional long seta in some specimens so that adults have either seven or eight long, hooked setae on each exopodite.

TERRESTRICYTHERE SP. (FIGS 22, 23)

Material examined

One adult male, with soft parts dissected in polyvinyl lactophenol stained with methylene blue and sealed in

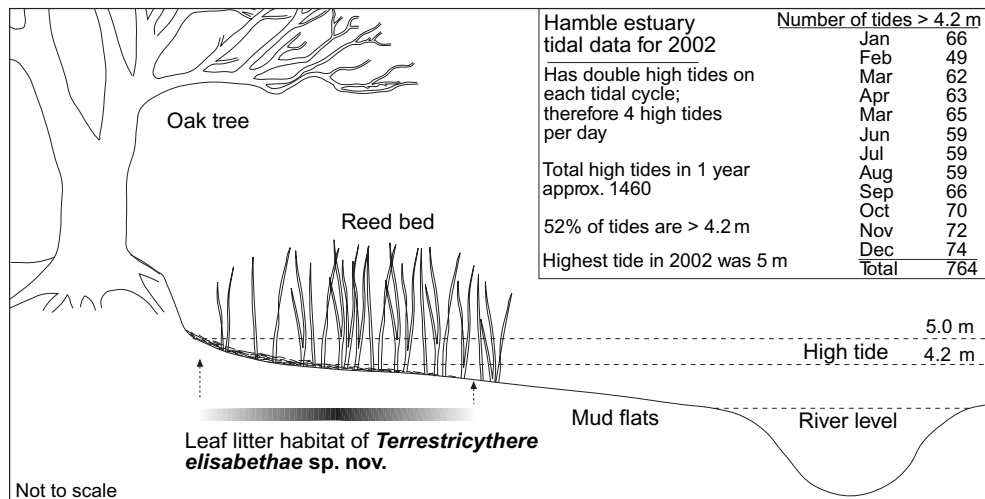**Figure 18.** Cross-section of the type locality of *Terristricythere elisabethae* **sp. nov.** and local tide data for 2002.
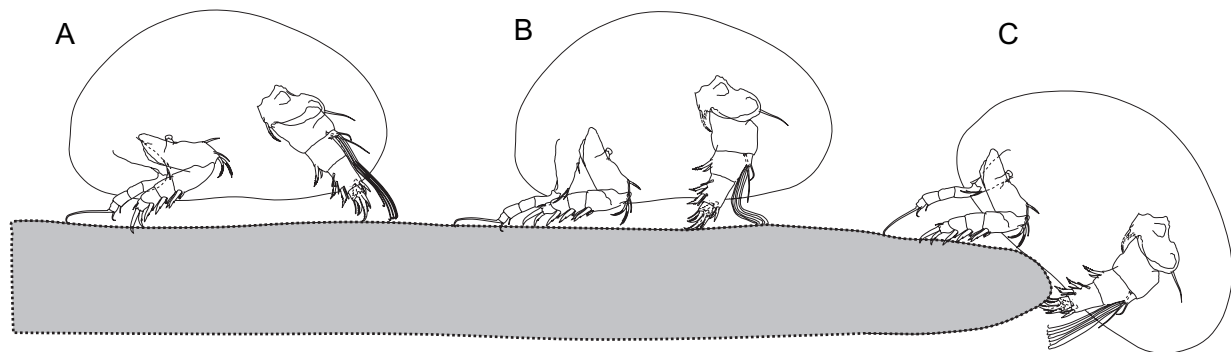

Figure 19. Locomotion in *Terrestricythere elisabethae* **sp. nov.** Only An2, L6 and L7 drawn for clarity.

a glass slide, and valves stored in a cavity slide (2003.1049); collected from a marine intertidal rock-pool at Gore Point, Porlock Bay, on the southern shore of the Bristol Channel, 51°14′N, 3°37′W, on 9 March 1978.

Remarks
Our specimen undoubtedly represents a fourth, hitherto undescribed species of *Terrestricythere*, but we consider it advisable to leave it in open nomenclature until additional material becomes available for a full description. The carapace shape is similar to that of the other *Terrestricythere* species but does not quite match any of them in lateral outline; relative to its length it is slightly less high than either *T. elisabethae* or *T. pratensis*, but slightly higher than *T. ivanovae*. The appendages are similar to those of other *Terrestricythere* species, the only significant differences being noted in the L7 and the hemipenis (Fig. 7). The An1 has five articulated podomeres, as in *T. elisabethae*

and *T. pratensis*. The L7 is most similar to that of *T. elisabethae*, bearing one long and one short-terminal claws, in contrast to the one long and one medium length claws of the two Russian species. The larger distal process of the hemipenis has an anvil-shaped protuberance on its outer edge (Figs 7, 23), similar to that seen in *T. pratensis*, but with rounded rather than pointed extremities.

LIFESTYLE OF *TERRESTRICYTHERE ELISABETHAE* SP. NOV.

Habitat
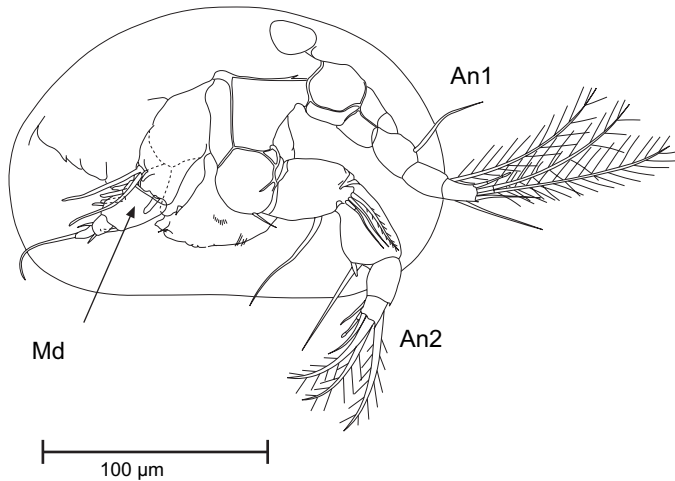*Terrestricythere elisabethae* sp. nov. has been recovered from the high part of the intertidal and salt marsh zones of two small tidally influenced rivers on the south coast of England. The habitats are shady and north facing and have patches of reeds growing along the mud banks of the rivers (Fig. 18). Oak and other deciduous trees grow just above the intertidal zone at both localities; trees overhang and provide

INSTAR	An1	An2	Md	Mx	L5	L6	L7	F
1 (A-8)	●	●	●					○
2 (A-7)	●	●	●	○				○
3 (A-6)	●	●	●	●				○
4 (A-5)	●	●	●	●	○			○
5 (A-4)	●	●	●	●	●	○		●
6 (A-3)	●	●	●	●	●	●	○	●
7 (A-2)	●	●	●	●	●	●	●	●
8 (A-1)	●	●	●	●	●	●	●	●
9 (A)	●	●	●	●	●	●	●	●

Terrestricythere elisabethae **sp. nov.** (Terrestricytheroidea)

INSTAR	An1	An2	Md	Mx	L5	L6	L7	F
1 (A-8)	First instar not recovered							
2 (A-7)	●	●	●	○				○
3 (A-6)	●	●	●	●				○
4 (A-5)	●	●	●	●	○			○
5 (A-4)	●	●	●	●	●	○		●
6 (A-3)	●	●	●	●	●	●	○	●
7 (A-2)	●	●	●	●	●	●	●	●
8 (A-1)	●	●	●	●	●	●	●	●
9 (A)	●	●	●	●	●	●	●	●

Neonesidea oligodentata (Kajiyama, 1913) (Bairdioidea)

Taken from Smith & Kamiya (2002)

INSTAR	An1	An2	Md	Mx	L5	L6	L7	F
1 (A-8)	●	●	○					
2 (A-7)	●	●	●	○				○
3 (A-6)	●	●	●	●				○
4 (A-5)	●	●	●	●	○			○
5 (A-4)	●	●	●	●	●	○		●
6 (A-3)	●	●	●	●	●	●	○	●
7 (A-2)	●	●	●	●	●	●	●	●
8 (A-1)	●	●	●	●	●	●	●	●
9 (A)	●	●	●	●	●	●	●	●

Eucypris virens (Jurine, 1820) (Cypridoidea)

Taken from Smith & Martens (2000)

INSTAR	An1	An2	Md	Mx	L5	L6	L7	F
1 (A-8)	●	●	●					○
2 (A-7)	●	●	●	○				○
3 (A-6)	●	●	●	●				○
4 (A-5)	●	●	●	●	○			○
5 (A-4)	●	●	●	●	●	○		●
6 (A-3)	●	●	●	●	●	●	○	●
7 (A-2)	●	●	●	●	●	●	●	●
8 (A-1)	●	●	●	●	●	●	●	●
9 (A)	●	●	●	●	●	●	●	●

Loxoconcha japonica Ishizaki, 1968 (Cytheroidea)

Taken from Smith & Kamiya (2003)

An1, antennule   L5, fifth limb
An2, antenna   L6, sixth limb   ● Limb resembling that of the adult
Md, mandible   L7, seventh limb   ○ *Anlage* of the limb
Mx, maxillula   F, furca

Figure 20. Summary of the appearance of limbs during ontogeny of ***Terrestricythere elisabethae* sp. nov.** and three representative species of the superfamilies Bairdioidea, Cypridoidea and Cytheroidea. *Neonesidea oligodentata* taken from Smith & Kamiya (2002), *Loxoconcha japonica* taken from Smith & Kamiya (2003), *Eucypris virens* taken from Smith & Martens (2000).

A-8 *Heterocypris bogotensis* Roessler, 1982
Cypridoidea

A-8 *Loxoconcha japonica* Ishizaki, 1968
Cytheroidea

A-8 *Terrestricythere elisabethae* sp. nov.
Terrestricytheroidea

Figure 21. The A-8 instars of ***Terrestricythere elisabethae* sp. nov.** and two representative species of Cytheroidea and Cypridoidea. *Heterocypris bogotensis* taken from Roessler (1983), *Loxoconcha japonica* taken from Smith & Kamiya (2003).

constant shade at one locality (River Cur), while at the other (Beaulieu River) there are trees close enough to provide shade during much of the day. Specimens were recovered among the reed beds, mostly from the leaf litter (predominantly oak and reed) that covers the surface of the mud, although a few have been found in the top few millimetres of the underlying sediment. The coast has double high tides during each tidal cycle so that there are four high tides a day. At the River Cur, there are approximately 1460 high tides a year, 52% of which are higher than 4.2 m, i.e. cover a significant proportion of the reed banks. There are periods of several days every month when high tides are too low to cover the reeds (neap tides), but the site is covered by brackish water on a regular basis. The salinity of the water in the River Cur ranges from 0 to 12‰. Salinities recorded in creeks on the Beaulieu River Estuary at the time of collection varied between five and 15‰.

Associated Foraminifera

Samples of leaf mould/litter and the underlying sediment from the reed marsh, within the habitat range of *Terrestricythere* (Fig. 18), were collected from near the highest high water at Curbridge on the River Cur (type locality), and at Jarvis Copse on the Beaulieu Estuary. Leaf mould alone was collected at Bailey's Hard on the Beaulieu Estuary. Live (stained with an aqueous solution of rose Bengal (1 g/l)) and dead (unstained) Foraminifera were picked separately from the residue using a moist paintbrush (therefore stained forms were clearly recognizable), the results being listed in Table 1 (x = present, xx = abundant).

Living forms were rare compared with dead forms, so it was not possible to make assemblage counts of >100 living individuals. Nevertheless, there is considerable similarity between the species present living at all localities (see Table 1; two samples were examined from Jarvis Copse, hence the range of values). How-

Figure 22. *Terrestricythere* sp. Adult male instar. A, right valve external. B, left valve external (Gore Point, Porlock) 2003.1049.

ever, *Ammonia limnetes* was common at Bailey's Hard but rare at the other localities. The dead assemblages comprised the same species with the addition of *Balticammina pseudomacrescens*. A further foraminiferal collection was subsequently undertaken by one of us (RJS) in November 2002, from leaf litter at Curbridge, within the upper range of *Terrestricythere* (and where the ostracod was particularly numerous). The Foraminifera were not stained so it is not possible to know for certain whether they were alive or dead. For the record, however, from a count of 50 specimens, the fauna comprised: *Balticammina pseudomacrescens* (17), *Trochammina inflata* (12), *Miliammina fusca* (10), *Haplophragmoides wilberti* (6), *Jadammina macrescens* (4) and *Elphidium williamsoni* (1). All these assemblages are typical of middle-high marsh (Horton, Edwards & Lloyd,1999).

Life cycle

Terrestricythere elisabethae sp. nov. has eight juvenile stages and one adult, a total of nine stages or instars. The high ratio of males to females (approximately 50 : 50) and the presence of sperm within some females indicates that it is a fully sexual species. Samples collected in May, June and November all yielded adults and juveniles. The May sample yielded a whole range of juveniles from A-8 to A-1. The later samples contained A-7 to A-1 juveniles (the A-8 instar was pos-
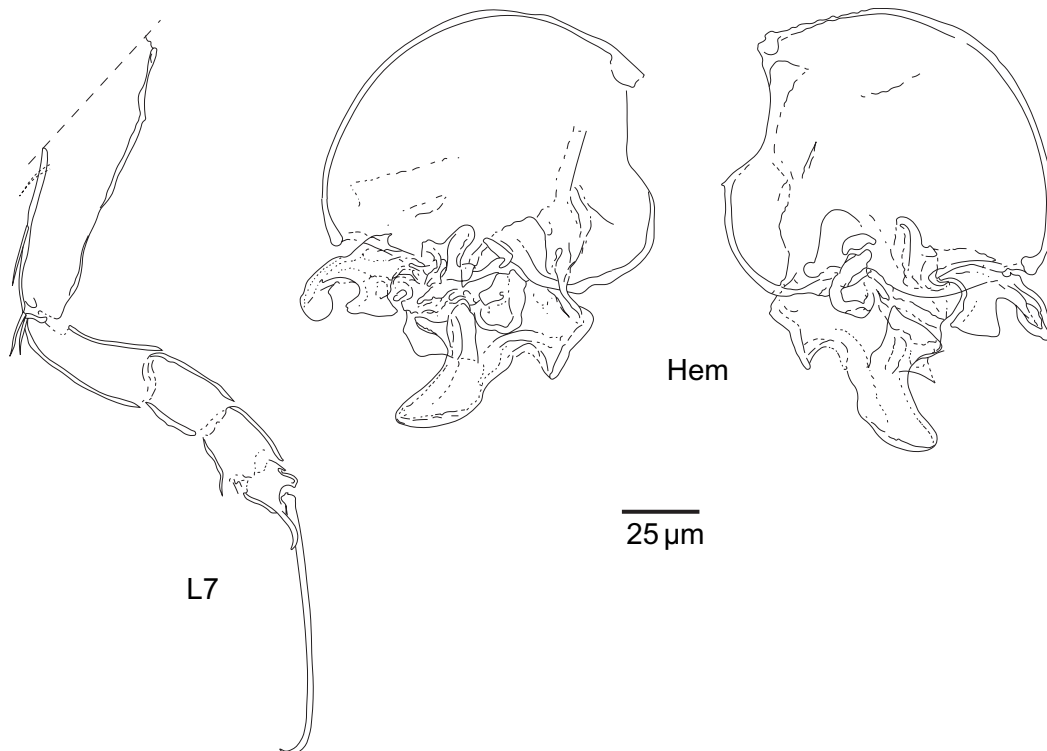

Figure 23. *Terrestricythere* sp. Adult male instar. L7 and Hem (Gore Point, Porlock) 2003.1049.

Table 1. Foraminifera associated with the habitat of **_Terrestricythere elisabethae_ sp. nov.**

	Living leaf mould	Living sediment	Dead % sediment
CURBRIDGE			
Miliammina fusca (Brady)	x	x	44
Haplophragmoides wilberti Anderson	x	x	32
Trochammina inflata (Montagu)	x	x	12
Jadammina macrescens (Brady)	x	x	9
Ammonia limnetes Todd & Brönniman	x	x	2
Balticammina pseudomacrescens Brönniman *et al.*	–	–	1
BEAULIEU, JARVIS COPSE			
Miliammina fusca (Brady)	x	x	19–40
Haplophragmoides wilberti Anderson	x	x	29–38
Trochammina inflata (Montagu)	x	x	12–21
Jadammina macrescens (Brady)	x	x	11–12
Ammonia limnetes Todd & Brönniman	x	x	0–3
Balticammina pseudomacrescens Brönniman *et al.*	–	–	4–11

	Living leaf mould	Dead % leaf mould
BEAULIEU, BAILEY'S HARD		
Miliammina fusca (Brady)	x	37
Haplophragmoides wilberti Anderson	x	11
Trochammina inflata (Montagu)	–	10
Jadammina macrescens (Brady)	x	12
Ammonia limnetes Todd & Brönniman	xx	29

sibly missed in these samples due to its very small size and translucent carapace). Although the sampling is limited, it suggests that this species may reproduce throughout the year. All samples were collected from the leaf litter, which indicates that this species breeds and lives its entire life in this habitat.

Mode of life
Terrestricythere elisabethae sp. nov. moves amongst the wet leaf litter, usually covered in a film of water (so thin as to be visible only under the microscope). Juveniles as young as A-7 also live on the surface of wet leaf litter, the smaller instars often present in between the striations of reed leaves. In the field, since the ostracods are white and the substrate is usually brown, individuals can often be detected with the naked eye and their identification verified with the aid of a 10× hand lens. A sample of leaf litter taken at the River Cur locality from a 20×20 cm area yielded 84 adults and juveniles, suggesting a population density of 2100 individuals m^{-2}. A laboratory culture has been successfully maintained for over a year in a sample of the habitat cut out with a knife in the field and placed in a plastic box (approx. 25×10 cm in plan, 5 cm deep) kept loosely covered with a lid to reduce moisture loss. Although a little water was added to the bottom of the box from time to time to replace loss by evaporation,

the mud/leaf surface of the culture remained out of the water at all times and ostracods could frequently be seen crawling on this surface.

The genus *Terrestricythere* Schornikov, 1969 was so named to reflect the presence of the type species in a terrestrial habitat. However, Schornikov (1980) did not consider any species of ostracod found in terrestrial habitats to be truly terrestrial animals, since they need water to respire. The habitat of *T. elisabethae* regularly undergoes submersion in brackish water, which strongly indicates that this species requires water to survive and is also not a true terrestrial animal. With each high tide that covers the site, the leaf litter is wetted and small pockets of water are left behind as the tide retreats. These small pockets of water allow tiny aquatic species to survive until the next submersion, including Foraminifera, copepods and the cytheroidean brackish ostracod *Loxoconcha elliptica* Brady, 1868.

Only occasional living specimens of *L. elliptica* have been found with our collections of *T. elisabethae*; the former is often extremely abundant in brackish-water salt marshes on British coasts and has an optimum salinity range of approximately 10–20‰ (Horne & Boomer, 2000); we suspect that higher population densities are likely to occur a little lower in the intertidal zone and further down the estuary in slightly higher

salinities (although this has not yet been investigated).

Terrestricythere elisabethae differs from *L. elliptica* (and indeed all aquatic ostracods) in that it is capable of moving around out of water, with water trapped inside and around its carapace. Specimens placed in a drop of water on a glass slide explore the drop, before sometimes leaving the drop pulling some of the water along with them. As they move the water moves with them, presumably due to the surface tension of the water. The densely spaced 'shaving brush' sensilla around the free margins of the valves probably aid in the retention of the water between the ostracod and the substrate and may even draw moisture up into the carapace through capillary action. The very long, stiff sensilla that protrude from the mid-region of the carapace may help to increase drag (or interact in some way with surface tension) so that more water is pulled along with the ostracod, and thus help to maintain the film of water around the ostracod.

As the water evaporates, movement reduces, until the ostracod starts moving in tight circles. When there is no longer water between the ventral margin and the substrate, movement stops altogether and the valves close, but usually with a small gape present. In this semidried state the ostracod can survive for a limited period (approximately 10 min in the laboratory at 15 °C). Once replaced in water the ostracod slowly recovers over a period of 5–10 min. The gape of the valves allows for water to enter the carapace and revive the animal and any air bubbles are slowly expelled by the appendages. Specimens in the laboratory that are dried for longer than approximately 10 min perish. It must be noted, however, that the temperature-controlled laboratory environment in which these observations were made has a high evaporation rate (a consequence of the air conditioning system) and specimens therefore probably dried out much more quickly than would normally be the case under natural conditions.

Harding (1955) considered that there are two kinds of organisms that can survive in terrestrial habitats, such as leaf litter. The first live in a film of water, while the second can live out of a film of water and are either dependent on a humid atmosphere or are desiccation-resistant. He suggested that the cypridoidean ostracod *Mesocypris terrestris* Harding, 1953 was of the second type due to its relatively large size (*c.* 1 mm in length) and globular shape, which he considered as being inconsistent with a lifestyle adapted to living in a film of water. He suggested that even though *M. terrestris* has a fully developed maxillular branchial plate (the part of the limb which, in aquatic ostracods, beats regularly to maintain a through-flow of oxygenated water within the carapace), it would not use it, as it is not an aquatic animal (Harding did not, however, study any live specimens).

Terrestricythere elisabethae has a lifestyle that is transitional between the two types of terrestrial lifestyles envisaged by Harding (1955). It needs water to respire and uses its maxillular branchial plate to create a current of water through the carapace (as confirmed by laboratory observations). However, it is not confined to films of water and can move across a dry substrate by taking a supply of water with it, in and around its carapace. Nevertheless, once this water supply is exhausted the ostracod ceases movement and risks death if not covered by water in the very near future. Thus it cannot be considered to belong to Harding's second group of organisms that can respire in air. The bushy setae of the ventral area of the carapace are probably an adaptation to hold water and reduce water loss as the ostracod transverses dry areas. The length of time that such water will last depends on the air temperature and humidity, and is at its greatest in damp, cool, shaded leaf litter, where this species lives. In conditions with very high levels of humidity we consider it possible that water may condense on the sensilla of the ostracod, replenishing its water supply and thus substantially increasing its survival time away from a body of water. The lifestyle of *T. elisabethae* could be termed epineustonic (i.e. an organism that lives above the water surface, but is in regular contact with it).

Locomotion

Terrestricythere elisabethae sp. nov. moves using the antennae, sixth and seventh limbs (Fig. 19). The long hooked setae of the antennal exopodite are fanned out in front and are used to help pull the ostracod along the surfaces of the leaves. The sixth limbs are used to push the ostracod along; a significant length of the anterior edge of the endopodite of the sixth limb comes into contact with the substrate during each walking movement, and the claws along this edge increase traction, as reported for *T. ivanovae* (Schornikov, 1980). This is different from the walking movement of other ostracods, for example cypridoideans, in which the long, curved claw of the sixth limb is used to roll the weight of the ostracod forward, so that the anterior edge of the endopodite of the sixth limb does not come into contact with the substrate (Kesling, 1951). When walking along a flat, horizontal substrate the seventh limbs are usually folded up along the body. However, occasionally the seventh limbs are also used to push the ostracod along in conjunction with the sixth limbs on horizontal surfaces, and on sloping or uneven surfaces the seventh limbs are used for extra grip. Specimens caught in the surface tension of the water use

the seventh limbs to try and hook on to an object and pull themselves free.

THE HINGE OF *TERRESTRICYTHERE*

The hinge of *Terrestricythere* (Figs 1H–N, 3A, B) is unique in the Ostracoda. In all ostracods the hinge provides the sole area of contact between the two valves when they are gaping, so that appendages may be extended for locomotion and other activities. Many Podocopida have distinctive hinge structures, ranging from simple anterior and posterior teeth separated by a median groove in one valve, which fit into corresponding terminal sockets and a median bar in the other valve (lophodont hinge), to more elaborate types with crenulate elements (e.g. merodont, entomodont) or strongly differentiated terminal teeth and sockets (e.g. amphidont) (see, for example, Athersuch, Horne & Whittaker, 1989).

According to our observations of a wide variety of living podocopids, these hinges function essentially as guides and locking devices to maintain the correct alignment of the valves in relation to each other. In podocopids with straight hinges, when the valves are gaping, contact is maintained along all or part of the median element, while the terminal elements become somewhat separated; the more complex or enlarged terminal elements of some taxa may serve to maintain or improve the contact between the two valves in the region of the terminal elements even when the valves are gaping.

In certain taxa with curved hinges (such as the podocopid *Xestoleberis*, with a merodont hinge; see, e.g. Whittaker, 1978) it is probable that only the central parts of the median elements, at the highest point of the convex dorsal margin, remain fully in contact when the valves are gaping; in such a case the function of the crenulate terminal elements can only be to lock the two valves together when closed (i.e. so that they cannot be rotated with respect to each other, about the plane separating the two valves). In *Terrestricythere*, on the other hand, there are interlocking terminal teeth and sockets but no interlocking median elements. There are two teeth on the RV, one situated towards the anterior and the other towards the posterior margin, and joined by a ridge running along the dorsal margin (Fig. 1M, N). The teeth interlock and move in two corresponding sockets on the hinge of the LV (Fig. 1K, L); the important difference, compared to all other ostracods, is that the larger LV, far from remaining in contact with the RV along its dorsal margin, actually *overrides* the RV dorsally when the valves are gaping (Fig. 3C, D). The terminal elements thus function more like true hinges than do those of any other ostracod genus.

This type of hingement is here formally named 'visordont' on account of its action being like that of a visor – the movable part of a helmet – which rotates on two distal pivots while sliding over the fixed part of the helmet. Exactly how this is achieved, without compromising the ability of the ostracod to seal itself off from the external environment when the valves are closed, remains unclear. Presumably there must be an unusually broad or flexible zone of the chitinous epicuticle in the dorsal region (Harding, 1965), which can accommodate the motion of the two valves sliding over each other.

AFFINITIES OF THE GENUS *TERRESTRICYTHERE*

Schornikov (1969) established the new family Terrestricytheridae, of equivalent status to other podocopid families such as the Bairdiidae and Cytheridae which are now considered in most schemes to be superfamilies. The majority of subsequent authors have given it superfamily status (e.g. Hartmann & Puri, 1974; Hartmann & Guillaume, 1996; Horne *et al.*, 2002).

Schornikov (1969) considered the family Terrestricytheridae to be closely related to the family Cytheridae Jones, 1850 (now equivalent to the superfamily Cytheroidea Jones, 1850) stating that most limbs, apart from the antenna and mandible, have a similar morphology to those of the Cytheridae. An important difference is in the nature of the antennal exopodite: in *Terrestricythere* the exopodite is a plate (or very reduced podomere) bearing eight long setae, totally unlike the 'spinneret seta' exopodite which constitutes a major synapomorphy of the cytheroidean families. There are also differences in the morphology of the thoracic limbs of the Terrestricytheroidea compared with the Cytheroidea. Additionally, the hinge is unique to the Terrestricytheroidea and distinctly different from that of any members of the Cytheroidea. The adductor muscle scar pattern of five scars arranged in a vertical row is superficially similar to that of the Bythocytheridae, the most ancient cytheroidean family, but in *Terrestricythere* the second and third scars from the bottom are diagonally offset from each other, suggesting derivation from a single scar. Hartmann & Puri (1974) suggested that this five-scar pattern is a derived character, while that of the Bythocytheridae is an ancient one. We consider these differences to be sufficient to justify maintaining a separate superfamily, the Terrestricytheroidea.

Maddocks (2000: 2, table 1), for unspecified reasons, preferred to consider *Terrestricythere* as representing a 'highly specialized' subfamily (Terrestricytherinae) of the family Cyprididae, superfamily Cypridoidea, rather than a family of the Cytheroidea or a superfamily in its own right. Martin & Davis (2001: 30) removed the Terrestricytheroidea from their classifi-

cation of Crustacea in the erroneous belief that Martens, Horne & Griffiths (1998) regarded terrestricytherids as modified candonids (superfamily Cypridoidea); Martens *et al.* indeed correctly pointed out that the genus *Terrestricypris* Schornikov, 1980 belongs to the Candonidae, but that it is neither the same as, nor even closely related to, *Terrestricythere*. Removal to the Candonidae, moreover, does not correspond to Martin & Davis' (2001: 64) classification table, where they included the Terrestricytheridae in the superfamily Cytheroidea.

In Maddocks' (2000) higher classification of Ostracoda the Cypridoidea comprises three families: the Cyprididae, Pontocyprididae and Macrocyprididae. We follow Horne *et al.* (2002) in regarding each of these as superfamilies of the suborder Cypridocopina, and the Cypridoidea as comprising four families: Cyprididae, Ilyocyprididae, Notodromadidae and Candonidae. The differences between these two schemes are more to do with rank than content. One of the most distinctive characteristics of the Cypridocopina (*sensu* Horne *et al.*, 2002) is the presence, in adult males, of a Zenker's organ, a relatively large, muscular sperm pump that is external to the copulatory appendage. The Sigillioidea (placed in a separate suborder Sigilliocopina by Horne *et al.*, 2002) also have a Zenker's organ. We cannot accept the assignment of *Terrestricythere* to any 'cyprid' group, whichever taxonomic hierarchy is preferred, because it lacks a Zenker's organ; in fact, it has a cytheroidean type of male copulatory appendage in which the sperm pump is incorporated within the hemipene.

The Terrestricytheroidea have some features that are shared by other superfamilies. For example, the reduced furcal rami are shared by the Cytheroidea, Darwinuloidea, and some species of the Cypridoidea. The antenna of *Terrestricythere* has three aesthetascs inserted proximally on the first endopodite podomere (Figs 2C, 5), in a similar position to a group of three or four aesthetascs (with apparently similar morphology) seen in the Darwinuloidea (see, e.g. Martens, 1998: fig. 4.7B). In *Terrestricythere* the mandibular basis (i.e. the proximal podomere of the mandible palp) bears a series of long, closely spaced setae with interlocking setules, forming a grating which could be interpreted as a filter screen; a remarkably similar feature is seen in Darwinuloidea (Martens, 1998: fig. 4.7C).

The robust, stout morphology of the antennule and the general morphology of the hemipenes are most similar to some species of Cytheroidea. The clasping hooks of the male fifth limbs are shared with the males of some taxa in the Cypridoidea, Macrocypridoidea, Pontocypridoidea, Cytheroidea and Sigillioidea (see, e.g. Horne *et al.*, 2002). The seventh limb is a modified walking leg and in some respects is mor-

phologically similar to that of the Cypridoidea, where it is a cleaning limb (see, e.g. Horne *et al.*, 2002: fig. 5). However, our observations have shown that the seventh limb in the Terrestricytheroidea is a specialized locomotory limb rather than a cleaning limb (see above). Which of these features are plesiomorphic and which are a result of convergent evolution is unclear.

The development of the furcal rami in early juveniles may shed some light on affinities between podocopan superfamilies. The furcal rami of the A-7 instars of the podocopids Terrestricytheroidea, Bairdioidea and Darwinuloidea, and the platycopid Cytherelloidea have a very similar morphology. In contrast, those of the podocopid Cytheroidea and Cypridoidea appear to be reduced (Fig. 25). From A-6 onwards the furcal rami in the Terrestricytheroidea and Bairdioidea gain another claw, whereas in Darwinuloidea they retain a similar morphology to that of the previous instar (Fig. 26). The Cytherelloidea gain two claws and therefore have the most developed furca of the species so far studied, perhaps representing a plesiomorphic form.

Analysis of the ontogenetic development of normal pore patterns is a useful tool for the determination of phylogenetic relationships (e.g. Tsukagoshi, 1989, 1990; Kamiya, 1997). In *T. elisabethae* sp. nov. the number of pore systems increases during ontogeny from three in the A-8 instar to a maximum of 153 in the adults. The adult maximum is comparable with many cytheroidean species, and less than cypridoidean and bairdioidean species (Ishizaki, 2001; Smith & Kamiya, 2002). A more useful comparison is that of the A-7 instar pore system patterns. As this feature is comparable in the very early stages of development it can help to shed light on the relationships between groups. The similarity between the superfamilies can be demonstrated by noting the differences (presences or absences) between the A-7 pore patterns, using representative species. *Terrestricythere elisabethae* sp. nov. has ten pores on each valve of the A-7 instar. This is a similar number to that of bairdioidean species, less than cypridoidean species and more than most cytheroidean species. Correlating pores between different species is open to some interpretation, but a possible correlation is given in Figure 27. *Terrestricythere elisabethae* sp. nov. has both pore B, which is absent in the 'typical' cytheroidean species (represented by *Loxoconcha uranouchiensis* Ishizaki, 1968), and pore C, which is absent in bairdioidean species. It lacks, however, pore J, which is present both in the cypridoidean and bairdioidean species, and pore L, present in cypridoidean species.

There is only one difference in the pattern between the Terrestricytheroidea and Cytheroidea–Loxoconchidae (the absence of pore B in *Loxoconcha uranouchiensis* Ishizaki, 1968). There are three differences
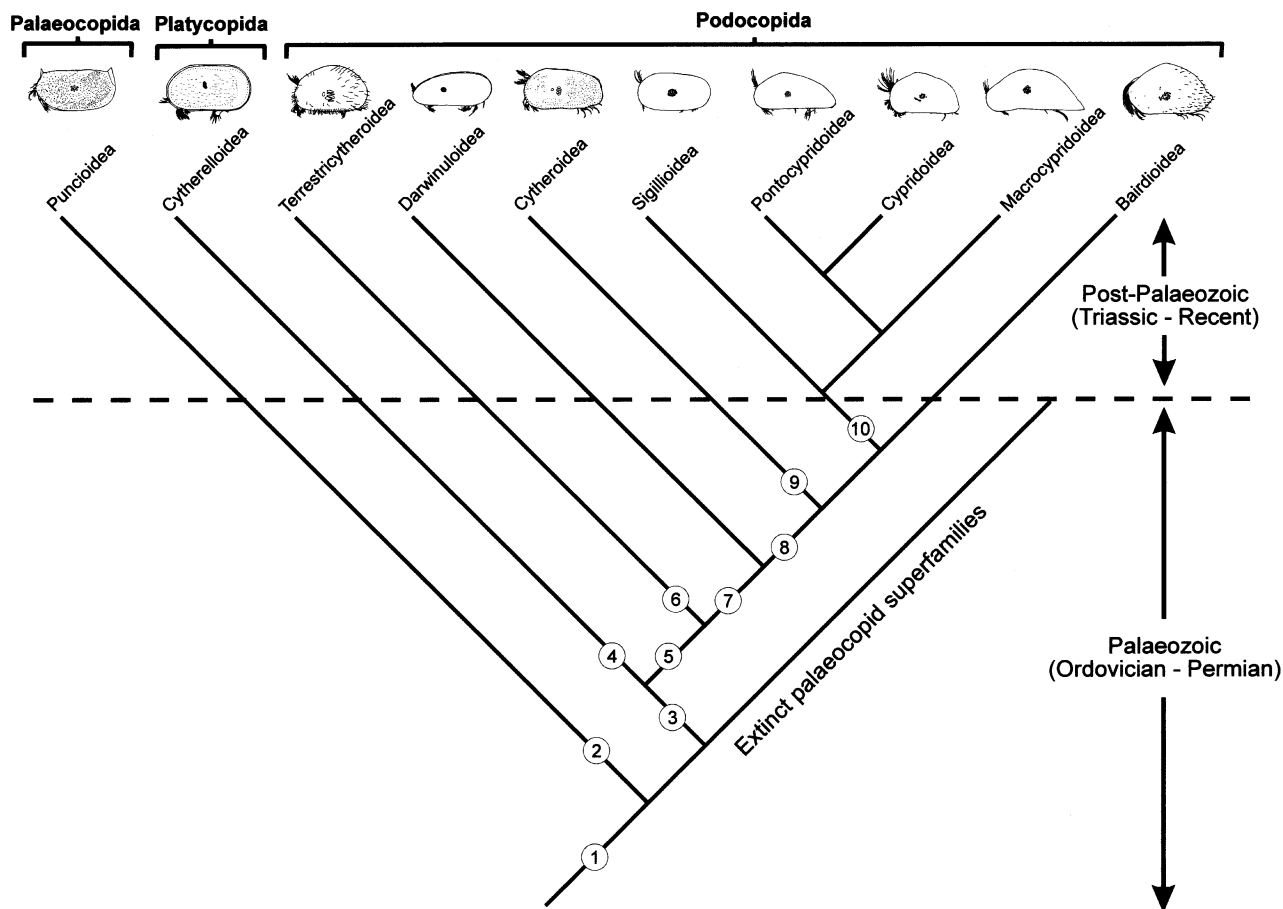
Figure 24. Tentative phylogram for the extant superfamilies of the Ostracoda, Podocopa. (1) Antennal exopodite with two podomeres, maxillular endopodite leg-like, eighth limb present in both sexes (= hypothetical Palaeozoic palaeocopid). (2) Reduction of antennal exopodite to a single elongate podomere. (3) Mandible palp bearing a filter comb with at least eight setae; maxillular endopodite a palp; loss of eighth limb (possibly represented by male copulatory appendage only). (4) Further development of filter combs on mandible and maxillula; loss of seventh limb. (5) Reduction of antennal exopodite to a short podomere or scale bearing setae. (6) Antennal exopodite bearing at least seven long setae. (7) Antennal exopodite bearing three setae. (8) Reduction of filter comb on mandible palp to four or fewer setae. (9) Development of antennal exopodite into a spinneret seta. (10) Development of a Zenker's Organ.

According to this hypothesis, the orders Podocopida and Platycopida had as a common ancestor a filter-feeding palaeocopid with an antennal exopodite with two podomeres, a mandible palp bearing a filter comb with at least eight setae, and an eighth limb represented only by the male copulatory appendage. Subsequently, the Platycopida became highly adapted to the filter-feeding mode of life while the Podocopida abandoned it and diversified as detritus-feeders, scavengers, carnivores and herbivores. The majority of the Palaeocopida, a highly diverse group in the Palaeozoic, became extinct at the end of the Permian; the only survivors, the puncioids, are highly derived forms in which only the leg-like maxillular endopodite and the presence of the eighth limb in both sexes are plesiomorphic. The origins of most extant superfamilies lie relatively early in the Palaeozoic, most probably in the Ordovician; the only post-Palaeozoic radiation at superfamily level was that of the Cypridocopina (Macrocypridoidea, Pontocypridoidea and Cypridoidea) from Sigillioidea that survived the end-Permian extinctions.

between the pore pattern of the Terrestricytheroidea and that of the Cytheroidea–Entocytheridae and Bairdioidea. Finally, there are four differences between the pore patterns of the Terrestricytheroidea and Cypridoidea. The Cytheroidea–Loxoconchidae are more similar to the Terrestricytheroidea than the Cytheroidea–Entocytheridae. This highlights the isolation of the specialized family Entocytheridae from other cytheroidean families as noted by Smith & Kamiya (2004). Thus in terms of pore patterns, the Terrestricytheroidea are more similar to 'typical' Cytheroidea species (i.e. excluding the very specialized Entocytheridae) than to the Bairdioidea or Cypridoidea.
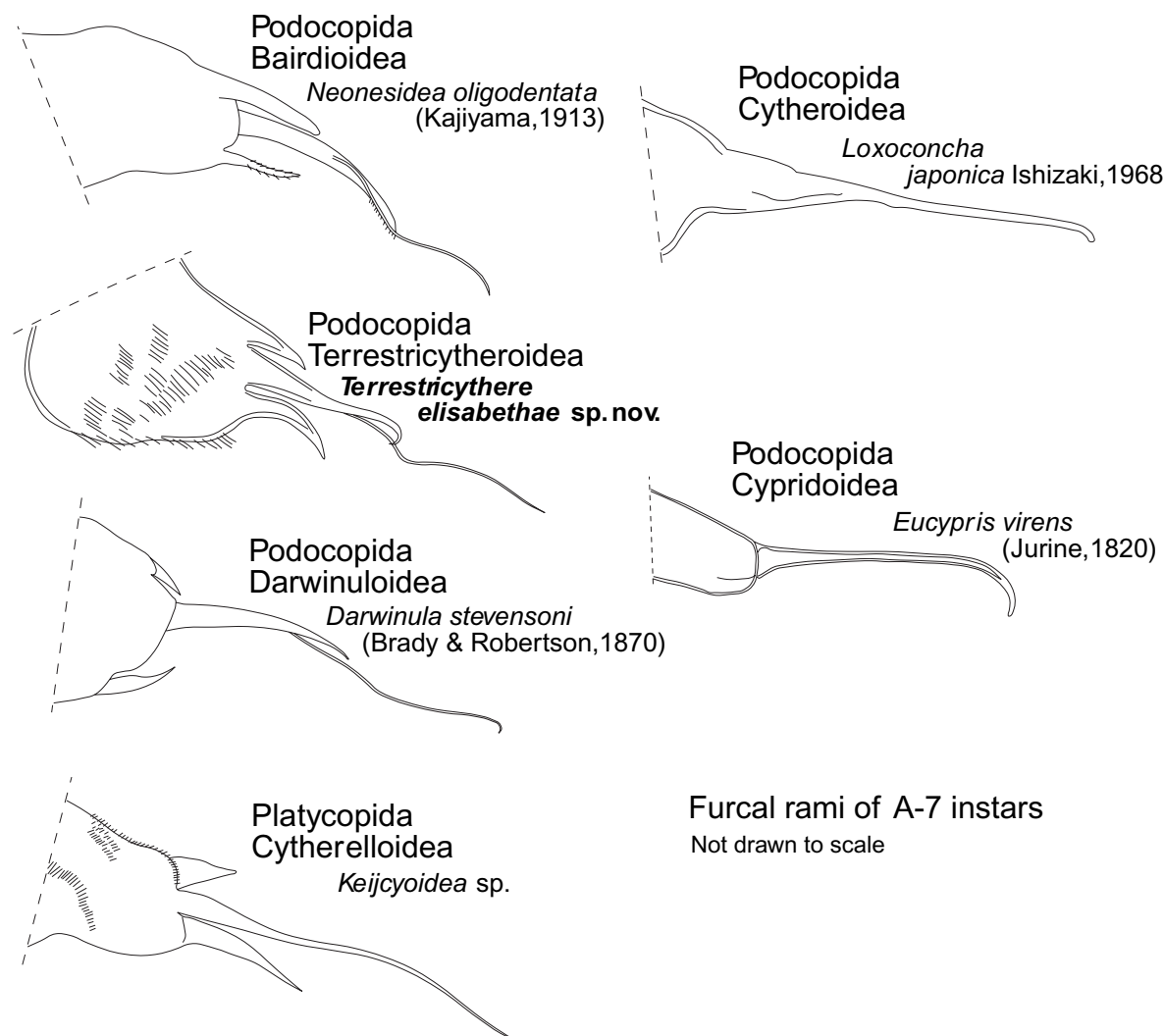
Figure 25. The A-7 instar furcal rami of ***Terrestricythere elisabethae* sp. nov.** and five representative species of the superfamilies Bairdioidea, Cypridoidea, Cytheroidea, Darwinuloidea and Cytherelloidea. *Neonesidea oligodentata* taken from Smith & Kamiya (2002), *Loxoconcha japonica* taken from Smith & Kamiya (2003), *Eucypris virens* taken from Smith & Martens (2000), *Darwinula stevensoni* original, *Keijcyoidea* sp. taken from Okada (2001).

The precise phylogenetic relationships between the major podocopan ostracod groups are still far from clear. One possible interpretation is illustrated in Figure 24, which is not the result of a formal cladistic analysis and is presented for discussion purposes only. From the considerations presented above we conclude that among the Podocopida the superfamily Terrestricytheroidea is probably most closely related to the Darwinuloidea and Cytheroidea, both of which originated in the Palaeozoic. We also note that it retains an A2 exopodite with a larger number of setae than any podocopan group except the Platycopina (also of Palaeozoic origin). We further posit that the superfamily Terrestricytheroidea, although it has no recognized fossil record, is likely to be of similar (Palaeozoic) age,

and suggest that fossil examples should be sought in marginal marine deposits from the Carboniferous onwards.

BIOGEOGRAPHY OF *TERRESTRICYTHERE*

Living populations (represented by large numbers of individuals) of *Terrestricythere* species have only been found in two parts of the world: the coastal regions of the NW Pacific (Kuril Islands and near Vladivostok) (Schornikov, 1969, 1980) and the coast of southern England (as described herein). As discussed above, we do not consider the record of two specimens from a lake in France (Scharf & Keyser, 1991) to be adequate evidence of a viable living population.
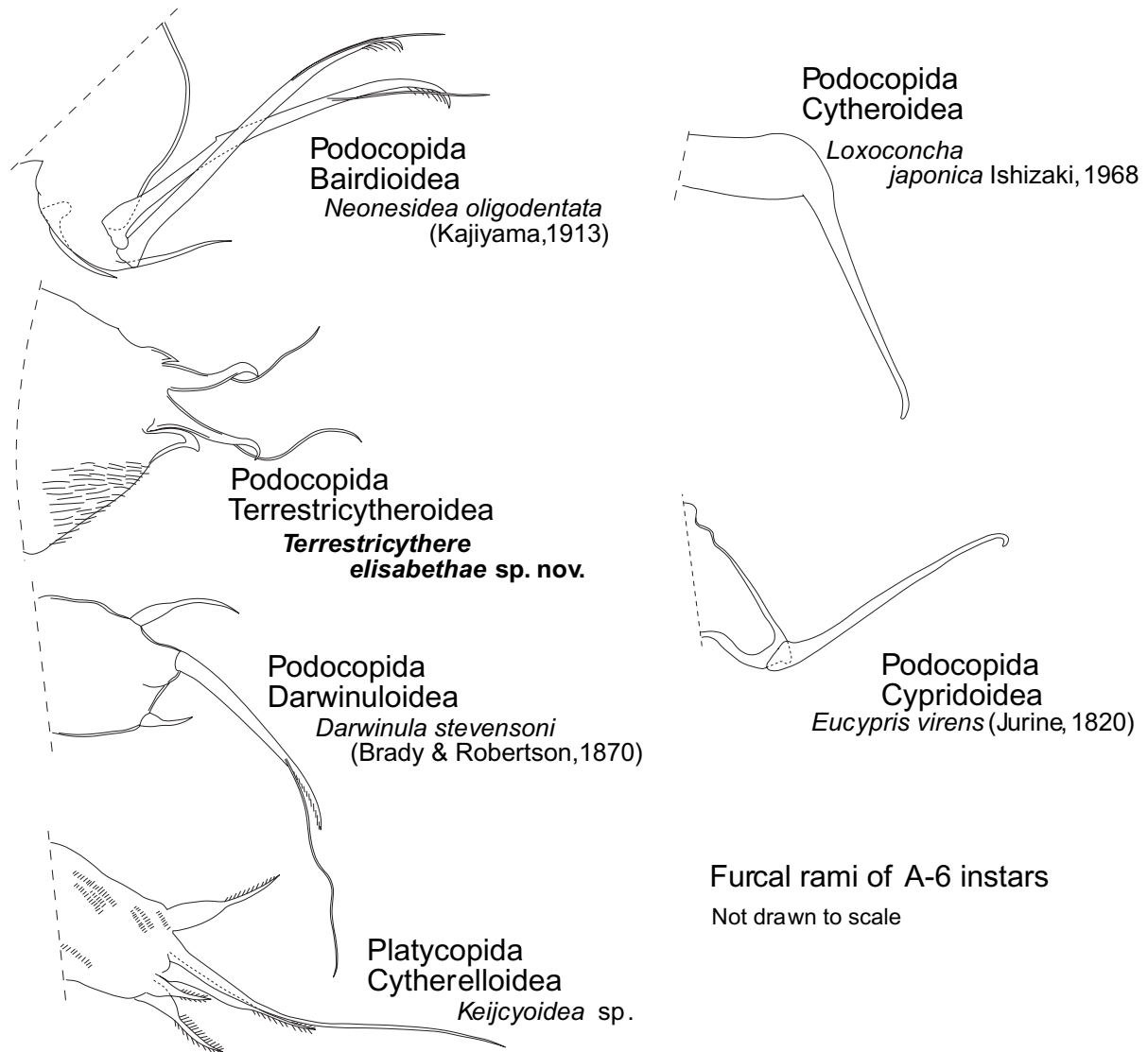
Figure 26. The A-6 instar furcal rami of ***Terrestricythere elisabethae* sp. nov.** and five representative species of the superfamilies Bairdioidea, Cypridoidea, Cytheroidea, Darwinuloidea and Cytherelloidea. *Neonesidea oligodentata* taken from Smith & Kamiya (2002), *Loxoconcha japonica* taken from Smith & Kamiya (2003), *Eucypris virens* taken from Smith & Martens (2000), *Uncinocythere occidentalis* taken from Smith & Kamiya (2004), *Darwinula stevensoni* original, *Keijcyoidea* sp. taken from Okada (2001).

This presents us with an interesting problem: do the English populations represent a hitherto unrecognized component of the native British fauna, or an invasion of an alien species? The fact that *Terrestricythere* has never previously been reported in the British Isles (in spite of more than a century and a half of collecting on British coasts by many ostracod specialists) could be explained by its unusual habitat, which is likely to have been ignored by those seeking ostracods, but it could also be an indication that it has been introduced to the area relatively recently. The northwest Pacific region is home to two known *Terrestricythere* species and, as little ostracod research has been done in that area, it could harbour more, perhaps being the centre of distribution of this genus. Its ability to survive in merely damp conditions for weeks or months would clearly be advantageous to transport by migrating birds (as has been proposed for cypridoidean ostracods with resting eggs; see, e.g. Horne & Smith, 2004), which, as we have already noted, would help to explain the isolated records in France and at Porlock.

Transport by human activity is another possibility, and we speculate that the transfer of amphibious mil-
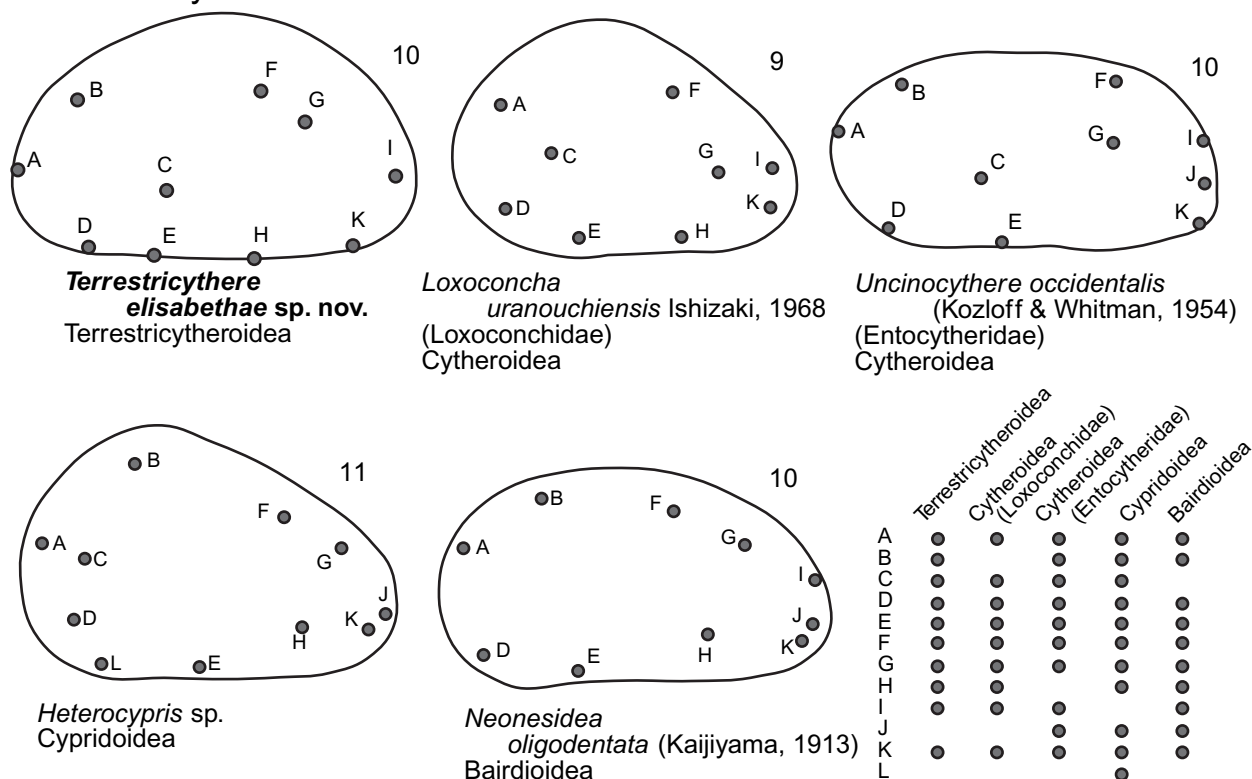
A-7 Pore Systems

Figure 27. The A-7 instar pore systems of **Terrestricythere elisabethae sp. nov.** and four representative species of the superfamilies Bairdioidea, Cypridoidea, Cytheroidea. *Neonesidea oligodentata* taken from Smith & Kamiya (2002), *Loxoconcha uranouchiensis* taken from Kamiya & Hazel (1992), *Heterocypris* sp. taken from Ishizaki (2001), *Uncinocythere occidentalis* taken from Smith & Kamiya (2004). Pore data for Darwinuloidea are unavailable.

itary vehicles and/or aircraft between the north-west Pacific and north-west Europe during World War II might have provided opportunities for introducing the ostracod to Britain. Whether *T. elisabethae* is a rare British endemic or a potentially damaging invader, it deserves greater attention than it has hitherto received.

ACKNOWLEDGEMENTS

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