

# A new tristichopterid (Osteolepiformes: Sarcopterygii) from the Mandagery Sandstone (Late Devonian, Famennian) near Canowindra, NSW, Australia

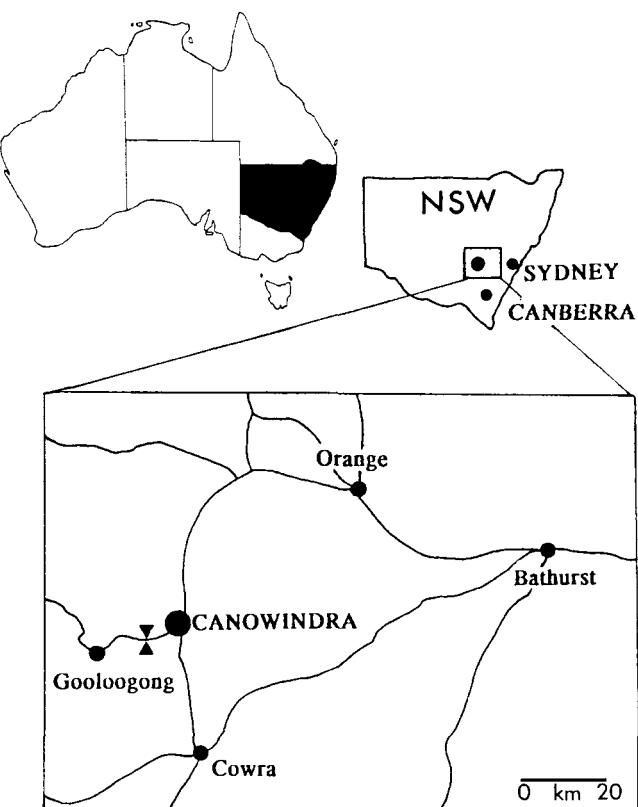
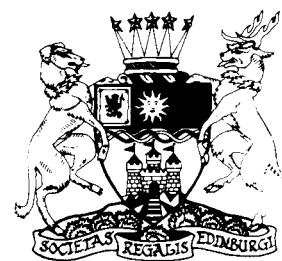
Zerina Johanson and Per Erik Ahlberg

**ABSTRACT:** A new member of the Tristichopteridae (=Eusthenopteridae), *Mandageria fairfaxi* gen. et sp. nov., is described from the Late Devonian (Famennian) Mandagery Sandstone outcropping near Canowindra, NSW, Australia. It is represented by several complete or partial heads and bodies, preserved as natural moulds. *Mandageria* shares derived characters with the Late Famennian tristichopterid *Eusthenodon wängjöi* from East Greenland; the pineal plate series is large and kite-shaped and is posterior to the middle of the parietals, the intertemporal does not contact the posterior supraorbital, a posterior process of the premaxilla divides the apical fossa, the anteriormost premaxillary tooth is enlarged, the postorbital is excluded from the orbit by a supraorbital-lacrimal contact, and the coronoids lack marginal teeth except posteriorly. *Mandageria fairfaxi* differs from *Eusthenodon* in superficial fusion of the supratemporal, tabular and postparietals, in the lateral extrascapulars being separated by only 2–3 mm in the midline anteriorly, and in having proportionately smaller scales. It also has an elongate supracleithrum, which is probably autapomorphic. The postcranial skeleton is comparable to that of the Frasnian genus *Eusthenopteron*, but differs in the more posterior position of the median fins, the poorly ossified vertebral column, and the flattened ectepicondyle. *Mandageria fairfaxi* is the second osteolepiform described from Canowindra (the first, *Canowindra grossi*) and, other than the now-reinterpreted *Marsdenichthys*, the first tristichopterid described from Australia.

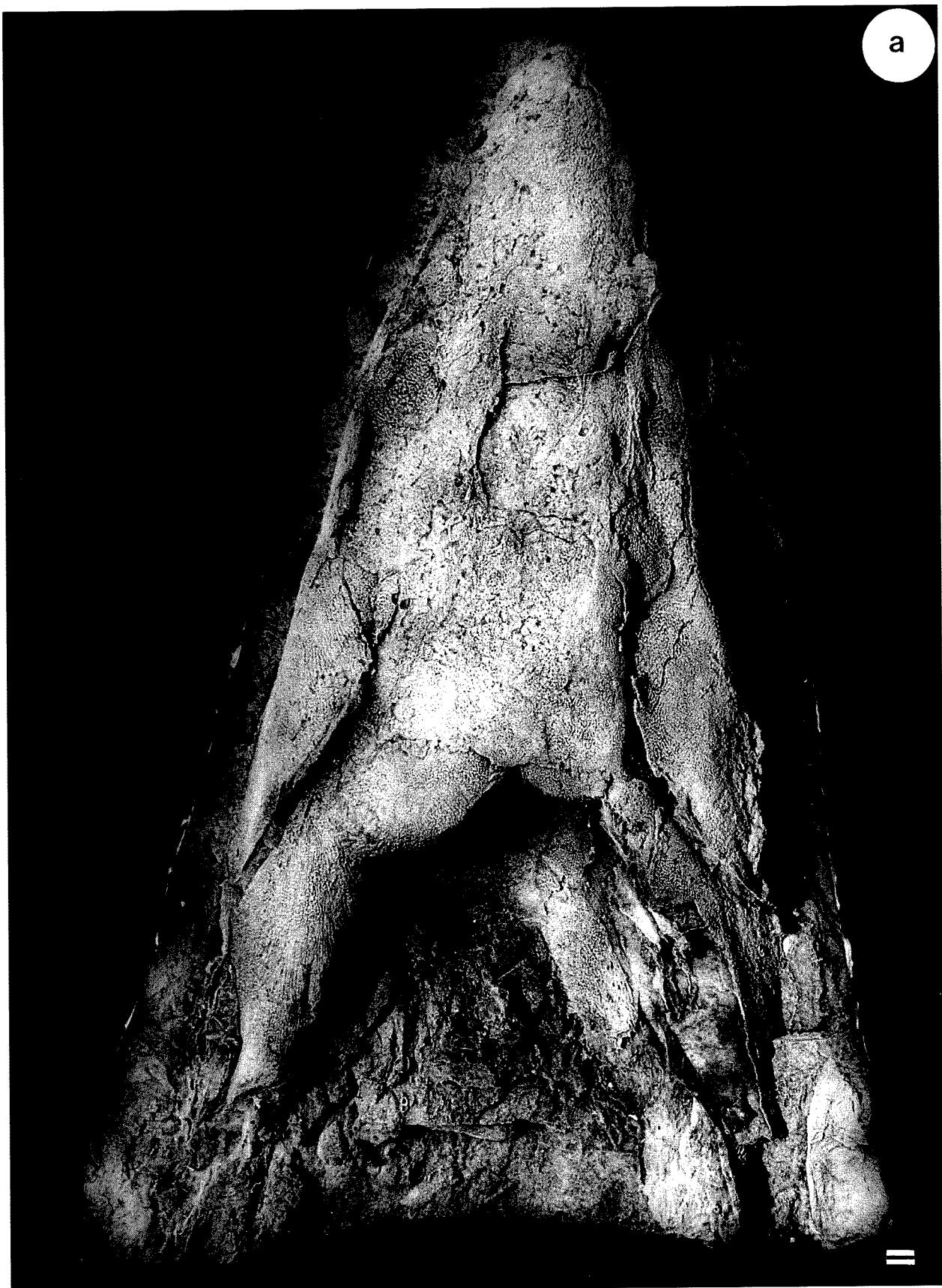
**KEY WORDS:** Devonian, *Mandageria*, *Eusthenopteron*, *Eusthenodon*, anatomy, relationships.

The Upper Devonian fauna from the Mandagery Sandstone was first discovered in 1956 during road repairs 10 km SW of Canowindra, New South Wales (Fig. 1). A large block was recovered, containing approximately 114 fish. The majority of these were placoderm fishes, but also present was a single specimen of the sarcopterygian *Canowindra grossi* Thomson 1973. In 1993, Alex Ritchie (Australian Museum, Sydney) relocated and excavated the Canowindra fossil layer, recovering 60–70 tonnes of quartzite slabs containing well-preserved fishes. These fish are preserved within a single stratigraphic layer, and it is believed they are part of a single community that became isolated in a pool of water of undetermined size. This pool dried, eventually killing the fish. These were then buried by incoming sediments with minor disturbance to the fish themselves, as indicated by the rarity of disarticulated placoderm plates or sarcopterygian scales.

Approximately 3000 fish have been collected from the Canowindra locality, most commonly the antiarchs *Bothriolepis* and *Remigolepis*. The arthrodire *Groenlandaspis* is also present, but rare. Also rare are the sarcopterygians, with the remains of approximately 20 individuals so far noted. Of these, only one taxon has been described, *Canowindra grossi*, known from a single specimen. Thomson (1973) was unable to determine if *C. grossi* belonged to the Osteolepiformes or the Porolepiformes, however, after additional preparation, Long (1985a) suggested that this taxon was an osteolepiform, with similarities to the Victorian genus *Beelarongia* Long 1987a. Young *et al.* (1992) later formalised this suggestion by assigning these genera to the Family Canowindridae along with the Antarctic taxon *Koharalepis* Young *et al.* 1992. It is



**Figure 1** Locality map of Upper Devonian (Famennian) fish fauna, near Canowindra, New South Wales, Australia. Fossil fish locality indicated by opposing triangles.



**Figure 2** *Mandageria fairfaxi*, F96508. Holotype, dorsal view of skull and shoulder girdle: (a) photograph; (b) (facing page) interpretative line drawing. This, the least distorted skull of *Mandageria*, shows an essentially natural outline in dorsal view. Note the extensive superficial fusion of the skull roof bones, and the presence of anamestic bones along the (apparently sutural and immobile) intracranial joint. Scale in this and all following photographs = 1 cm. Graphic conventions for this and all other line drawings: thick outline—true margin; dotted thick outline—probable course of true margin; dashed thick outline—reconstructed true margin; thin outline—broken edge; vertical hatching—broken surface (except in Fig. 6 where it denotes missing pieces in the dermal bone cover); horizontal interrupted hatching—scale cover; circles—matrix; smooth shading—jointed part of lepidotrichia (except in Fig. 14b, where it denotes preserved part of gill skeleton).

interesting to note that *C. grossi* possesses a tuberculate scale pattern which has not been observed on any other individual sarcopterygian at Canowindra.

Devonian osteolepiforms are known from several other Australian localities. Of these, the best known are from the Mount Howitt locality, Victoria, yielding *Beelarongia patrichae* and the rhizodopsid (Long, pers. comm. 1995) *Marsdenichthys longioccipitus* Long 1985b. Other Australian taxa include *Gogonasus andrewsae* Long 1985c from the Gogo Formation,

Western Australia, and *Gyroptychius* cf. *G. australis* (Young & Gorter 1981) from Hatchery Creek, NSW. These two taxa have been assigned to the Family Osteolepididae, a paraphyletic taxon (Long 1985a–c) requiring extensive revision. Other unidentified sarcopterygian materials have been noted from several Australian localities (Young 1993, appendix 1). New sarcopterygian materials from near Eden, NSW, are currently being excavated by the authors and Alex Ritchie.

Four sarcopterygian species, including *Canowindra grossi*,

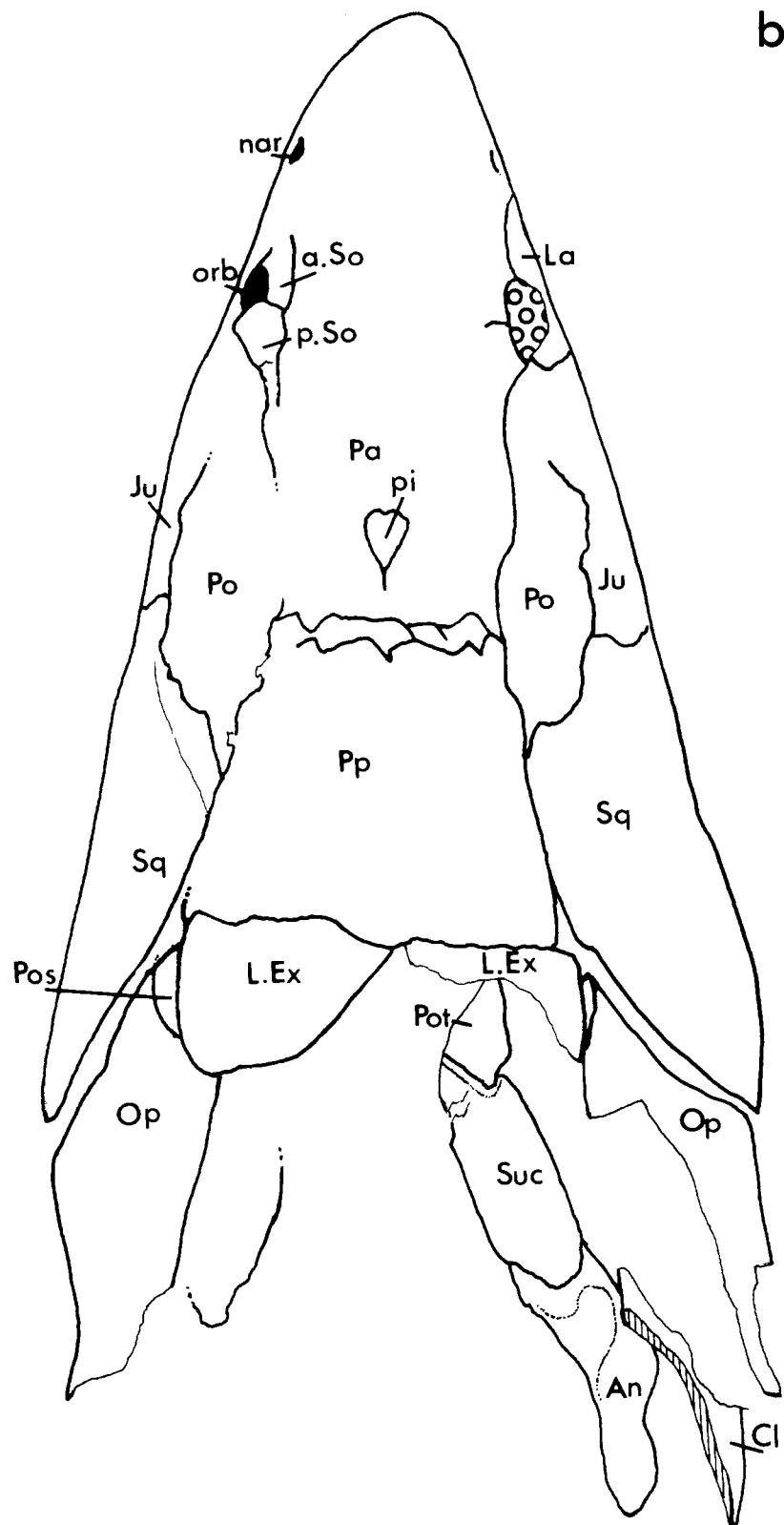
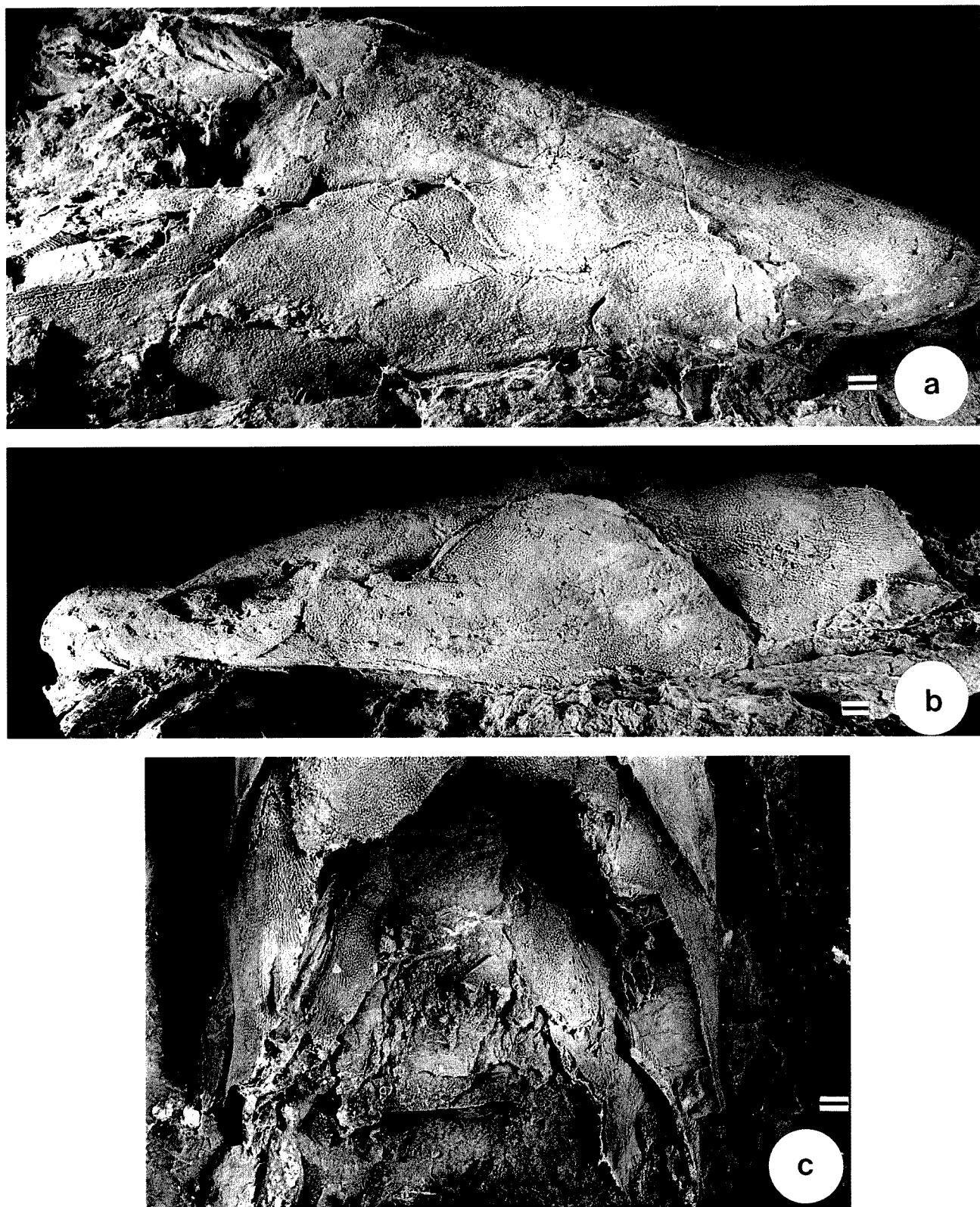


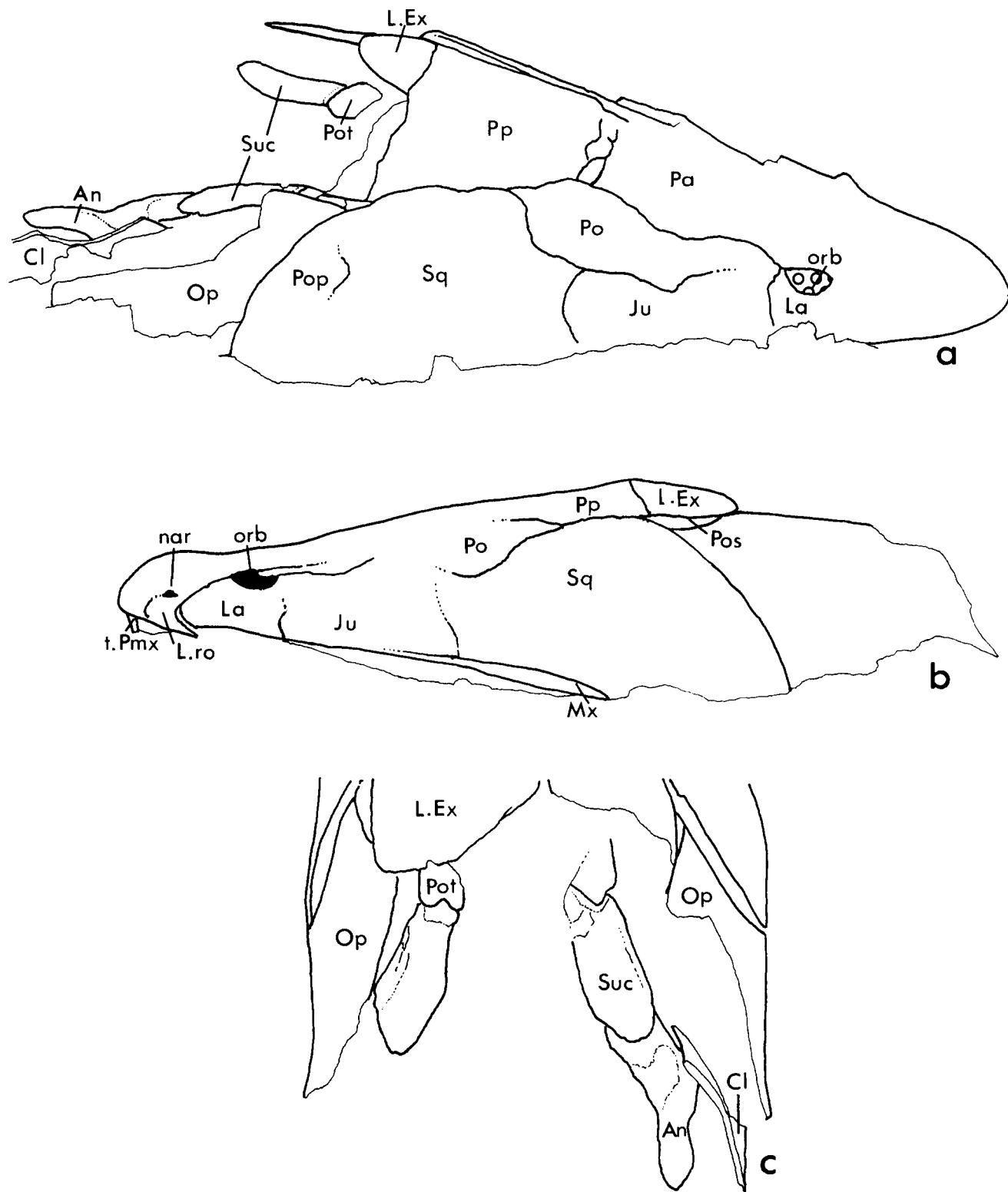
Figure 2 (continued)



**Figure 3** *Mandageria fairfaxi*, F96508. Holotype: (a) skull in right dorsolateral view; (b) skull in left lateral view; (c) shoulder girdle in dorsal view. The skull is slightly compressed dorsoventrally, disrupting the junction between skull roof and cheek. In (c), note the long supracleithrum and the correspondingly short ornamented area on the anocleithrum.

are present in the Canowindra fauna. Two of these species are members of the Tristichopteridae Cope 1889 (this is a senior synonym of Eusthenopteridae Berg 1940). The first of these is described below and compared to other members of the Tristichopteridae. The second tristichopterid from Canowindra will be described at a later date, but some characters of this taxon will be discussed below. Tristichopterids are character-

ised by the presence of a postspiracular bone, a three-lobed caudal fin, the anteroposterior orientation of the crista parotica, absence of an extratemporal, and round, non-cosmoid scales with a median ridge on the inner surface (Jarvik 1980; Long 1985b; Young *et al.* 1992; Cloutier & Ahlberg 1996). Only the first two of these characters are likely to be synapomorphies; the third is of uncertain distribution,



**Figure 4** *Mandageria fairfaxi*, F96508. Holotype. Interpretative line drawings of photographs in Figure 3. Graphic conventions as in Figure 2.

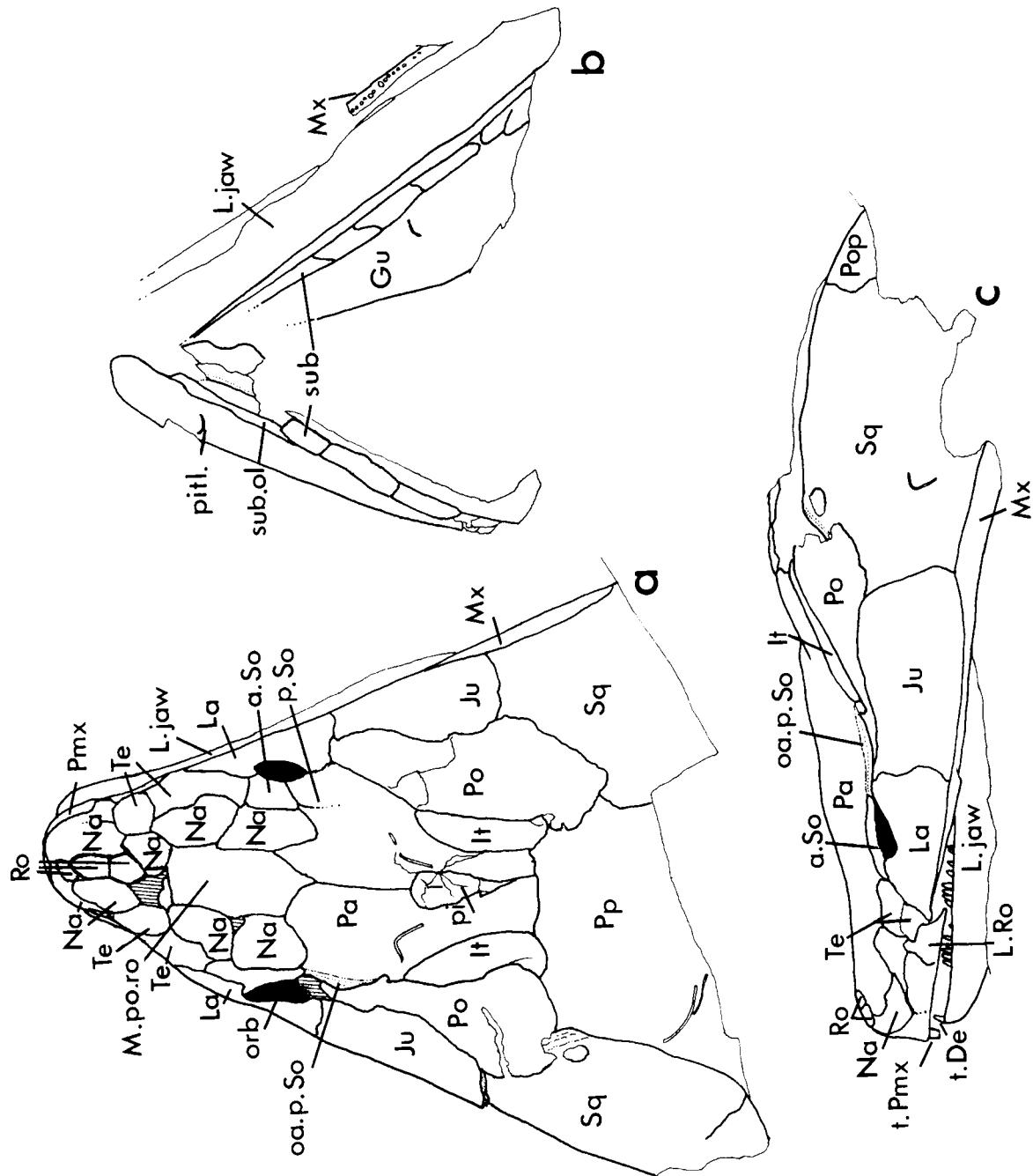
whereas the fourth and fifth are more widely distributed among the Osteolepiformes.

The material from Canowindra consists overwhelmingly of natural moulds, filled with hardened sandstone casts and a greasy clay which presumably represents chemically weathered bone. Very occasionally, patches of hard bone survive in specimens from the deeper parts of the site. The specimens are prepared, in most instances, by chiselling out and retrieving the sandstone endocasts and washing and brushing the clay

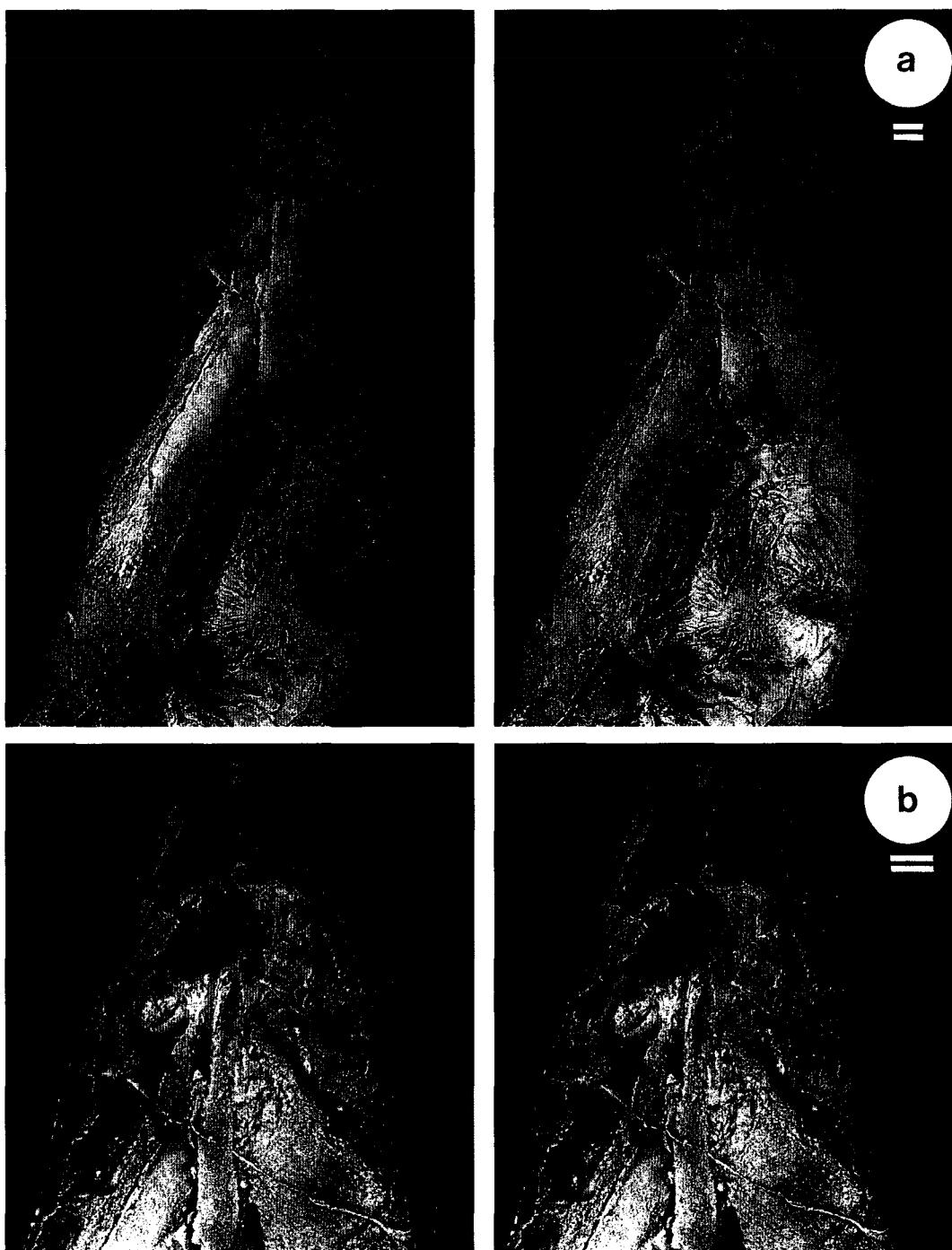
away to expose the hard and fine-grained natural moulds. Some of the endocasts preserve valuable information on the internal cranial and branchial anatomy of these fishes, and are preserved for study. Latex casts are then taken from the natural moulds, whitened with ammonium chloride, and photographed. Labelled line drawings were made from these photographs. Fibreglass replicas of all specimens figured or mentioned in this paper have been registered and deposited at the Australian Museum, Sydney. Due to the size and weight



Figure 5 *Mandageria fairfaxi*. (a) F96857a, anterior part of skull roof in dorsal view. (b) F96857b, lower jaws and gular series in ventral view. (c) F96857a, left cheek in lateral view. This specimen provides the clearest picture of the bone pattern on the snout.



**Figure 6** *Mandageria fairfaxi*. Interpretative drawings of photographs in Figure 5. (a, c) F96857a. (b) F96857b. Graphic conventions as in Figure 2. In (c), the dotted vertical line in the snout represents a break that can be interpreted either as a suture, or as a crack following the course of the supraorbital sensory canal.



**Figure 7** *Mandageria fairfaxi*, F96855c. (a) Palate and internal view of posterior skull roof, stereo pair. (b) Closeup of anterior part of palate, stereo pair.

of the sandstone slabs, original specimens will remain in Canowindra, to be housed in a planned 'Age of Fishes' museum.

Institutional abbreviations. AM F, Palaeontology Section, Australian Museum, Sydney; BMNH, Department of Palaeontology, Natural History Museum, London; MGUH, Geological Museum of the University of Copenhagen, Denmark.

## 1. Systematic palaeontology

Subclass SARCOPTERYGII Romer 1955

Order OSTEOLEPIFORMES Berg 1937

Family TRISTICHOPTERIDAE Cope 1889

*Mandageria* gen. nov.

**Diagnosis.** As for type and only species.

**Etymology.** For the Mandagery Sandstone.

**Type species.** *Mandageria fairfaxi*.

*Mandageria fairfaxi* sp. nov.

**Diagnosis.** A large tristichopterid, up to 1·6 m long, having a narrow and acutely pointed head, very small and numerous scales, lateral extrascapulars which almost meet in the midline anteriorly, elongate supracleithra, and premaxillae which are separated from the anteriormost postrostral by the anteriormost nasals. The ventral hyomandibular articulation is much posterior to the dorsal articulation.

**Remarks.** The Tristichopteridae is a clade defined by the possession of a postspiracular bone. Members of the group also share a number of other characteristics, such as a relatively long ethmosphenoid cranial block and a trifurcate or diamond-shaped tail, but these features also occur in certain

other osteolepiforms. Among the tristichopterids, *Mandageria* resembles *Eusthenodon wängsöji* in lacking a contact between the posterior supraorbital and intertemporal, and in having the jugal and postorbital excluded from the orbital margin. The braincase of *Mandageria* will be described separately in a forthcoming paper.

**Etymology.** In honour of Mr James Fairfax, Sydney, for his generous support of scientific research on the Canowindra fish fauna.

**Holotype.** Australian Museum F96508, an almost complete specimen including skull roof, lower jaws, body (flattened), pectoral fin skeleton, caudal fin.

**Locality.** 10 km SW of Canowindra, NSW, on the road to Goologong.

**Horizon.** Mandagery Sandstone, Upper Devonian.

### 1.1. Referred material

F96855a–d, dorsal skull roof with associated palate, branchial arches and partial lower jaws; F96897, dorsal skull roof with associated right pectoral fin, postcranial scales and posterior vertebrae; F96857, nearly complete skull roof and anterior lower jaws; F96861, left ventral surface preserving posterior part of mandible, gular, clavicle, cleithrum, pectoral fin and scales; F96903, ventral portion of caudal fin and anal fin; F96854a, b, nearly complete skull roof and anterior lower jaws, missing are posterior portion of postparietal shield, opercular series and extrascapular series; F96895, partial pectoral fin preserving humerus and scapulocoracoid; F96899, caudal fin; F98592a, b, palate with partial internal surface of skull roofing bones, gill arches and partial gular series; F98593a, b, palate with partial braincase, gill arches and partial gular series; F98593, dentaries, gular series, clavicle, postcranial scales; F98720, scales; F98721, braincase, with gill arches. Specimens are referred to *Mandageria fairfaxi* on the basis of general morphology, scale morphology, size and dermal ornament.

## 2. Description

The following description covers all known aspects of the anatomy except the braincase, which is still under preparation and which will be described in a separate paper.

### 2.1. Skull

**2.1.1. Gross morphology.** *Mandageria fairfaxi* has a narrow head with an acutely pointed snout (Fig. 2), in contrast to other tristichopterids which are somewhat more broad-snouted. In lateral view, the least distorted skull (F96508) shows a faintly concave profile just behind the snout, giving the head an outline somewhat like the toe of a boot. The parietal–postparietal boundary, and thus presumably the supracranial joint, is relatively posterior in position. In F96508, the parietal shield (incorporating the parietals and all dermal snout bones) is 2·1 times as long as the postparietal shield, compared with 2·4 times in *Eusthenodon* (reconstruction, Jarvik 1952), 2·2 times in the second tristichopterid from Canowindra, and 1·8 times in *Eusthenopteron* (reconstruction, Jarvik 1952).

**2.1.2. Premaxilla and maxilla.** The lateral contact between the premaxilla and the maxilla is best preserved on the left side of F96857 (Figs 5c, 6c), where it is visible posteroventral to the nasal opening. It can also be seen on the left side of F96508 (Figs 3b, 4b). In shape and position it compares closely with the same structure in *Eusthenopteron* (Jarvik 1980, fig. 122) and *Eusthenodon* (Jarvik 1952, fig. 26A). Anteriorly, the premaxilla is deep; the posterior part of the bone seems to be almost wholly concealed behind a pair of lateral rostral

bones, but this region is difficult to interpret (see nasals, rostrals and tectals, below).

A large tooth, similar in size to the palatal fangs, is present at the anterior edge of the premaxilla close to the midline of the snout. This tooth is visible on F96508 and F96857, but is difficult to photograph on these specimens. The premaxillary tooth is best observed on F96855c (Figs 7, 9). We refer to this as a ‘tooth’ rather than a fang, because it is not paired with a replacement pit; the fangs of the palate, coronoids and dentary occur in closely integrated pairs which show alternate replacement. The enlarged tooth lies at the labial margin of the premaxilla, in line with the premaxillary tooth row. One specimen preserving a palatal view, including the apical fossa (F96855c, Figs 7, 9), shows a broad, tapering, posteriorly directed process which springs from the anterior end of the premaxilla (that is, adjacent to the midline of the skull) and divides the apical fossa in two. The proximal end of this process supports the enlarged premaxillary tooth. The apical fossa is deep, and the process slopes down into it, unlike in megalichthyids (see below) where a comparable process extends straight posteriorly at the level of the premaxillary tooth row.

A very similar enlarged premaxillary tooth can be seen in an undescribed specimen of *Eusthenodon wängsöji* from East Greenland (MGUH field no. 1337), and in *Eusthenodon* material from Andreyevka-2 in Russia (Lebedev, pers. comm.). The second tristichopterid from Canowindra also displays this feature, although less strongly developed. By contrast, there is no enlarged tooth *Eusthenopteron* (Jarvik 1980) or *Platycephalichthys* (Vorobyeva 1977). Among other sarcopterygians, a comparable tooth occurs in the rhizodonts *Strepsodus* (Andrews 1985) and *Barameda* (Long 1989) and in the megalichthyids *Ectosteorachis* (Thomson 1964), *Megalichthys* (Jarvik 1966), and *Cladarosymblerma* (Fox *et al.* 1995). In *Ectosteorachis* and *Megalichthys* the tooth is carried on an interpremaxillary or on a premaxillary process and is situated posterior to an unbroken premaxillary tooth row. The premaxillary process extends into the apical fossa, nearly dividing it into two in these taxa. In *Cladarosymblerma*, the premaxillary process is shorter and the enlarged tooth lies within the tooth row (Fox *et al.* 1995). Interestingly, a posterior process which divides the apical fossa and sutures with the vomer is also present in the tetrapods *Acanthostega* (Clack 1994) and *Crassigyrinus* (Clack 1996 and pers. comm.). In *Greererpeton* (Smithson 1982), the fossa is divided by a process of the vomer reaching forwards to contact the premaxilla. None of the tetrapods has enlarged teeth associated with the process.

The maxilla is not well preserved in specimens assigned to *Mandageria fairfaxi*, as it is frequently shifted and displaced under more dorsal bones. There does not appear to be any great difference between the maxilla of *Mandageria* and those of other tristichopterids. Like in *Eusthenodon* (Jarvik 1952), but unlike *Eusthenopteron* (Jarvik 1980), there is no significant dorsal ‘corner’ or process of the maxilla at the junction between jugal and squamosal. *Platycephalichthys* has an intermediate morphology (Vorobyeva 1962). Outgroup comparison with osteolepidids (e.g. Fox *et al.* 1995; Lebedev 1995) shows that *Eusthenopteron* displays the primitive character state.

**2.1.3. Lacrimal and jugal.** The lacrimal is very similar to those of *Eusthenopteron* (Jarvik 1980) and *Eusthenodon* (Jarvik 1952). Like the latter, but unlike the former, it reaches up posterior to the orbit to contact the posterior supraorbital (i.e. F96857a, Figs 5c, 6c). The jugal is rectangular in shape and is larger than the lacrimal. Young *et al.* (1992, p. 66, fig. 47) argued that a similar size of the lacrimal, jugal and postorbital was a synapomorphy for the Tristichopteridae,

Osteolepididae and Megalichthyidae, while a jugal at least twice as long as high (such that the lacrimal, jugal and postorbital were dissimilar in size) was a synapomorphy of the Canowindridae. In *Mandageria fairfaxi*, the jugal is longer than wide, and the lacrimal, jugal and postorbital are dissimilar in size, however, the size of the jugal does not approach that seen in the Canowindridae. The taxonomic utility of these types of 'size characters' is questionable, particularly when some taxa show an intermediate condition.

**2.1.4. Postorbital.** The orbits of *Mandageria fairfaxi* are relatively small and situated in the anterior third of the headshield. The postorbital is elongate anteroposteriorly, very narrow anteriorly and widening posteriorly from a point one-third of the length from the anterior edge. The posterior margin is rounded and ends beyond the anterior margin of the postparietal shield. The anterior end of the postorbital is excluded from the orbital margin by a connection between the posterior supraorbital dorsally and lacrimal laterally. This condition is also seen in *Eusthenodon wängsöji* (Jarvik 1952, fig. 26A), and in a slightly different form (jugal-supraorbital contact) in the second tristichopterid from Canowindra (Ahlberg & Johanson, in review) and in *Eusthenodon* sp. from Andreyevka-2, Russia (Lebedev, pers. comm.). It appears to be a synapomorphy of these genera, setting them apart from *Eusthenopteron* (Jarvik 1980) and *Jarvikina* (Vorobyeva 1977), in which the postorbital still reaches the orbit. The postorbital is also excluded from the orbital margin in the Canowindridae (Young *et al.* 1992, fig. 44C), but this is most probably a homoplasy with the tristichopterids.

**2.1.5. Squamosal and preopercular.** The posteroventral corner of the cheek is not preserved on any specimen of *Mandageria fairfaxi* so the morphology of the quadratojugal is unknown. The anterior margin of the squamosal consists of two gently concave sutural edges for the postorbital and jugal; the former faces anterodorsally, the latter anteroventrally. The dorsal and posterodorsal edges of the squamosal form a smooth curve which continues posteriorly to become the posterior edge of the preopercular. The suture between the squamosal and preopercular is difficult to trace, but is indicated in F96508 (Figs 3a, 4a) by a faint line which extends ventrally for a short distance, makes a small anterior curve, and then resumes its ventral course.

This squamosal morphology is similar, not only to that in other tristichopterids (Vorobyeva 1977; Jarvik 1980), but also to that in the osteolepidids *Osteolepis*, *Thursius* and *Gyroptychius* (Jarvik 1948). It is clearly the generalised osteolepiform condition. Long (1987a, p. 840) noted that an irregular six-sided squamosal is a unique feature of the Osteolepiformes (taken by him to include the Tetrapoda). However, as this morphology results from a combination of certain characters which are primitive for the Sarcopterygii (retained squamosal-maxillary contact) with others which are derived within the group (squamosal-quadratojugal contact), it is doubtful whether it can be defined as a character in its own right (Ahlberg 1991).

Only the dorsalmost part of the preopercular is visible. It is a narrow, upright bone, a characteristic which Long (1985b, 1987a) also suggested to be unique to the Osteolepiformes (including Tetrapoda). We concur with this interpretation.

**2.1.6. Nasals, rostrals, and tectals.** The bones of the anterior part of the headshield are best preserved on F96857 (Figs 5a, 6a), and the following description is based on this specimen. The median postrostral is large with a V-shaped posterior margin. Three smaller rostral bones extend along the midline anterior to the median postrostral. The median postrostral is flanked on each side by two fairly large nasal bones.

The bone pattern on the anterior part of the snout contains

areas of ambiguity, as the course of the supraorbital lateral line cannot be observed directly. At the tip of the snout, a pair of fairly large crescent-shaped bones suture with the dorsal margins of the premaxillae and meet in the midline (thus preventing the anteriormost rostral from touching the premaxilla). These must be the anteriormost bones of the nasal series. The next pair of nasal bones must therefore be the oval elements which lie between these crescentic bones and the midline row of three small rostral bones. Immediately posterior to these is a transverse row of four elements (one partly displaced as to leave a hole in the skull roof; Figs 5a, 6a), which abut posteriorly against the large median postrostral and the nasals which flank it. This transverse row of four bones can be interpreted in two ways: either the two middle bones are rostrals and the two lateral bones are nasals, or the middle bones are nasals and the lateral are tectals. The latter interpretation is shown in Figure 14a, but there are no obvious criteria for choosing between the two.

The narial opening is single, small, slightly elongated with distinct anterior and posterior notches, and visible in dorsal view. The suture pattern in the narial area is again difficult to interpret. On the left side of F96857a, two apparent vertical sutures can be observed on the upper jaw margin anterior to the rear end of the premaxilla (Figs 5c, 6c). The posterior of these two sutures can also be recognised on the left side of F96508 (Figs 3b, 4b), where it can be seen to form the anterior margin of a small bone which occupies the space between the nares and the jaw margin. This bone is clearly a lateral rostral corresponding to that of *Eusthenopteron*. Dorsal to this bone, but slightly overlapping it, lies another small element in F96857a. This is a tectal bone, and its ventral margin carries a notch which in life formed the dorsal margin of the naris. The tectal bone appears to have broken into a smaller ventral and larger dorsal piece, separated by a horizontal crack, but it is possible that this 'crack' is in fact a suture separating two tectal bones. It may be that the tectal element(s) separates the lateral rostral and anterior supraorbital.

The vertical suture which defines the anterior edge of the lateral rostral reaches almost to the jaw margin. As the horizontal suture between the lateral rostral and the premaxilla cannot be detected, we can infer that there is at most a very narrow premaxillary exposure along the jaw margin. Most probably, the premaxilla lies internal to the lateral rostral; this is certainly the relationship between the adjacent maxilla and lacrimal.

While the posterior of the two apparent vertical sutures on the upper jaw margin can be easily accounted for as marking the anterior edge of the lateral rostral, the anterior 'suture' is more difficult to interpret. In other osteolepiforms there is no suture in this area, as the facial lamina of the premaxilla extends unbroken from the suture with the lateral rostral to the tip of the snout (i.e. Jarvik 1980, fig. 116A). It would be tempting simply to dismiss it as an artefact, but the fact that it is present on both sides of the snout in F96857a strongly suggests that it represents a genuine structure of some kind. This could be a suture, in which case *Mandageria* has two lateral rostrals on each side, a unique snout pattern among osteolepiforms. However, it is also possible that it is a crack which follows the course of the supraorbital sensory canal. In this case, *Mandageria* has a normal osteolepiform snout pattern.

These ambiguities cause problems when comparing *Mandageria* with other tristichopterids. The presence of two lateral rostrals (if correctly inferred) is an obvious autapomorphy. Lack of contact between the lateral rostral and anterior supraorbital was interpreted by Young *et al.* (1992, fig. 47, character G1) as a synapomorphy characterising the Family

Eusthenopteridae (= Family Tristichopteridae). The separation of the anteriormost postrostral from the premaxillae by the anteriormost nasals is again autapomorphic (compare *Eusthenopteron*, Jarvik 1980; *Eusthenodon*, Jarvik 1952; *Platycephalichthys* and *Jarrikina*, Vorobyeva 1977). Given that the bone pattern of the snout is subject to individual variation and even asymmetry, it is doubtful whether a more detailed analysis would yield characters of taxonomic value.

**2.1.7. Parietal, supraorbitals and intertemporal.** The suture separating the parietal bones is not readily visible on most specimens. The pineal opening is present, but very small; it is covered by a kite-shaped series of small bones and is close to the posterior margin of the parietals (Figs 5a, 6a, 10a, 10c). In this respect *Mandageria* resembles *Eusthenodon* (Jarvik 1952, fig. 26B), but differs from *Eusthenopteron* and *Jarrikina* which have more anteriorly placed pineal openings surrounded by rounded or oval series of pineal plates. The condition in *Platycephalichthys* (Vorobyeva 1962, 1977) is uncertain. The middle part of the parietal carries a curved pit line. The ratio of the parietal to postparietal length is 0·99 for *Mandageria fairfaxi*; 1·11 for *Eusthenopteron* (Jarvik 1980, fig. 120); 1·32 in *Eusthenodon* (Jarvik 1952, fig. 26B) and 1·3 for *Jarrikina* (Vorobyeva 1977, fig. 42B). This contrasts with the ratio of parietal shield to postparietals (see Section 2.1.1.) and shows that the parietals form an unusually small part of the parietal shield in *Mandageria*.

The intertemporal, which is intimately sutured to the lateral margin of the parietal, is elongate and extends anteriorly to a point midway along the lateral edge of the parietal shield, but does not contact the posterior supraorbital (Figs 5, 6). Among the Tristichopteridae, this separation of the intertemporal and posterior supraorbital by the parietal is seen only in *Eusthenodon* (Jarvik 1952, fig. 26B), and is not present in the second tristichopterid from Canowindra (Ahlberg & Johanson, in review). Thus, this character is probably a synapomorphy grouping *Mandageria fairfaxi* and *Eusthenodon*, and separating these from all other tristichopterids. Three small anametic bones separate the parietal from the postparietal shield in F96508 (Fig. 2); whether this is a general feature of the species is uncertain. Similar anametic bones are seen in some specimens of *Eusthenopteron* (Jarvik 1980, fig. 119).

Anterior and posterior supraorbitals are present in *Mandageria fairfaxi*. The posterior margin of the posterior supraorbital narrows posteriorly to a sharp point, but is separated from the intertemporal by the parietal (see above). The shape of the posterior supraorbital matches that in *Eusthenodon*, *Jarrikina* and the second Canowindra tristichopterid (Ahlberg & Johanson, in review), whereas the corresponding bone in *Eusthenopteron* lacks the elongate posterior corner. The anterior extent of the anterior supraorbital is difficult to establish, and the presence of a connection between this bone and the anterior tectal (a synapomorphy of the Tristichopteridae [Young *et al.* 1992]) cannot be established with confidence.

**2.1.8. Postparietal shield.** The postparietal shield of *Mandageria* comprises the postparietal, tabular and supratemporal; there is no extratemporal. Although the sutures between these bones have become superficially fused externally, they can readily be distinguished on the internal surface of the postparietal shield (F96855b, Figs 11a, 12a). In internal view, the postparietal shield compares very closely with those of *Eusthenopteron* (Jarvik 1980, fig. 118), *Platycephalichthys* (Vorobyeva 1977, pl. XIV:1) and the Russian *Eusthenodon* material from Andreyevka-2 (Lebedev, pers. comm.). The most obvious feature is a strong ridge which runs anteroposteriorly along the surface of the tabular and onto the supratemporal. This ridge probably marks the position of the crista parotica.

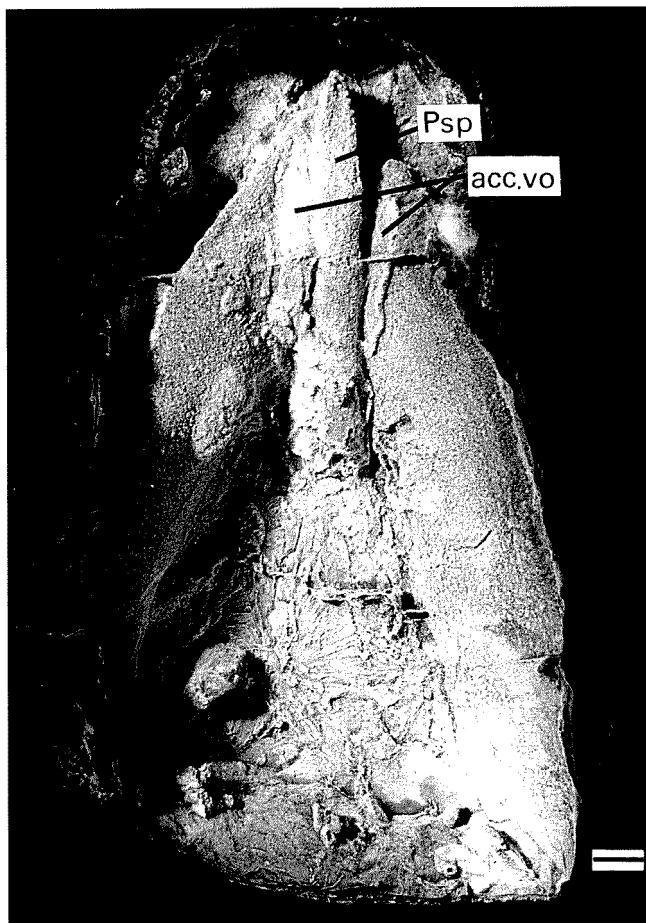
Another conspicuous characteristic of the inner surface is a smooth area which bounds the spiracular notch anteromesially; this too is paralleled in other tristichopterids. The postparietal shield of *Mandageria* is relatively narrow. The width/length ratio is approximately 1·4, compared with 1·37 in *Eusthenopteron* and 1·75 in *Eusthenodon*. Transverse pitlines are present on the posterior half of the postparietal, but the course of the lateral line canals cannot be determined.

**2.1.9. Extrascapulars.** In *Mandageria fairfaxi*, the lateral extrascapulars, which carry pit lines and overlap onto the median extrascapular in the usual osteolepiform manner, are three-sided with almost straight anterior and lateral margins but smoothly convex posteromesial margins. They almost meet in the midline anteriorly, being separated by a gap of 2–3 mm. The same morphology occurs in canowindrids (Thomson 1973; Long 1985a, 1987a; Young *et al.* 1992) and in rhizodonts (Andrews 1985; Long 1989).

Young *et al.* (1992, p. 61) argued that this condition is primitive for the clade (Rhizodontida [Osteolepiformes + Tetrapoda]). They stated that it is present not only in canowindrids and rhizodonts, but also in megalichthyids, *Lamprotolepis* Vorobyeva, 1977 and *Thysanolepis* Vorobyeva, 1977. The contrasting derived condition, four-sided lateral extrascapulars which are well separated in the anterior midline, was said by them to occur in tristichopterids and in osteolepidids such as *Osteolepis* and *Gyroptychius*.

Clearly, *Mandageria* does not fit well into this scheme. In order to evaluate it more fully, it is helpful to break the character into two, namely 'three-sided lateral extrascapulars' and 'lateral extrascapulars almost meeting in midline'. Among tristichopterids, *Mandageria* is the only form known to possess both these characters. The second Canowindra tristichopterid also has three-sided lateral extrascapulars (Ahlberg & Johanson, in review), but these are widely separated in the midline. *Eusthenopteron* is shown by Jarvik (1980) as having four-sided lateral extrascapulars. However, in specimens BMNH P6797 and P60337 (the only ones available to us which show the extrascapulars clearly), the lateral extrascapulars are arguably three-sided, and the whole extrascapular layout, including the separation of the mesial edges of the lateral extrascapulars, is scarcely distinguishable from that in the second Canowindra tristichopterid. Similarly, in *Eusthenodon wängsöji*, Jarvik (1952) reconstructs four-sided lateral extrascapulars, even though they are three-sided in at least one specimen (Jarvik 1952, fig. 23). The lateral extrascapulars of *Eusthenodon* sp. from Andreyevka-2 are three-sided (Lebedev, pers. comm.). The condition in *Platycephalichthys* is uncertain, while the extrascapulars of *Jarrikina* have only been figured as a reconstruction (Vorobyeva 1962, 1977). We conclude that the generalised condition among tristichopterids is to have well separated lateral extrascapulars; the shape of these may primitively be three-sided within the group, but this is more difficult to determine.

Turning now to other osteolepiform subgroups, we agree with Young *et al.* (1992) regarding the condition in canowindrids and rhizodonts. However, the occurrence of four-sided lateral extrascapulars in the megalichthyid *Cladarosymblema* (Fox *et al.* 1995) contradicts Young *et al.*'s interpretation of the Megalichthyidae, and we feel that insufficient evidence has been presented for the condition in *Lamprotolepis*. This character complex clearly needs further consideration. However, for the present we interpret *Mandageria* as autapomorphic within the Tristichopteridae (homoplastic with the Canowindridae and Rhizodontida) in having lateral extrascapulars which almost meet in the midline. The general character complement of *Mandageria* strongly suggests that it is a derived member of the Tristichopteridae, deeply nested



**Figure 8** *Mandageria fairfaxi*, F98592a. Palate, showing 'accessory vomers'.

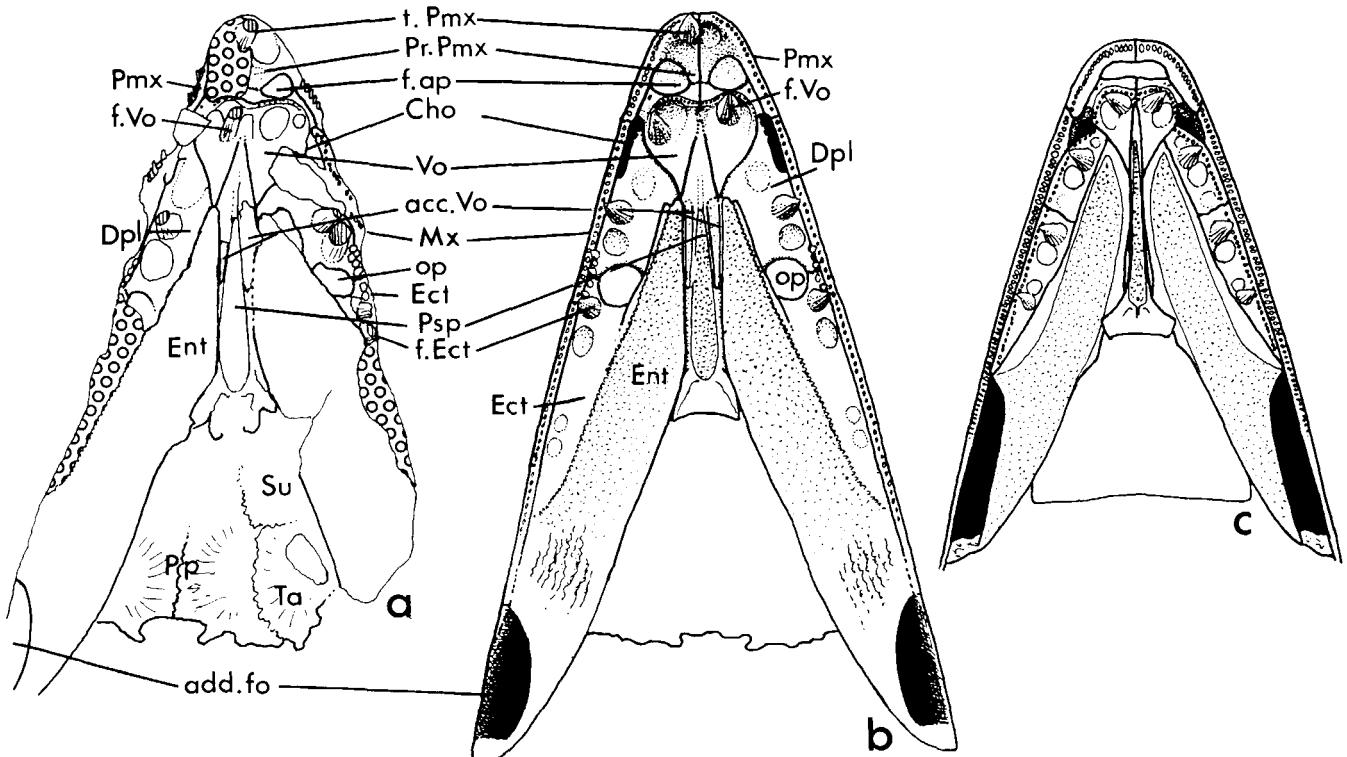
within the group, and recent phylogenetic analyses of the authors support this conclusion.

Lateral to the lateral extrascapulars is the postspiracular bone, the presence of which is considered to be a synapomorphy for the Tristichopteridae (Jarvik 1980; Long 1985b); it has been observed in *Eusthenopteron*, *Mandageria fairfaxi*, the second tristichopterid from Canowindra (Ahlberg & Johanson, in review), and has been inferred in *Eusthenodon* (Jarvik 1952). In *Mandageria fairfaxi* the postspiracular sits entirely between the lateral extrascapular, opercular, preopercular and squamosal, unlike in *Eusthenopteron* (Jarvik 1980, fig. 121A), where it also extends anteriorly between the squamosal and the tabular.

**2.1.10. Operculogular series.** The operculogular series resembles those of *Eusthenopteron* (Jarvik 1980) and *Eusthenodon* (Jarvik 1952) very closely. It comprises opercular, subopercular, submandibulo-branchiostegal, submandibulars (probably seven), lateral gulars, and a small median gular plate (Figs 5b, 6b, 17). This pattern is also seen in osteolepidids (Jarvik 1948, 1980; Lebedev 1995) and seems to be primitive for the Osteolepiformes as a whole. Compared to *Eusthenopteron*, the opercular of *Mandageria* is somewhat larger and more rectangular.

**2.1.11. Palate.** The palate of *Mandageria fairfaxi* is associated with the skull roof in F96855c (Figs 7, 9) and is also preserved on F98592a and F98593. In this latter specimen, the palate is associated with braincase material and gill arches (Fig. 13), and will be figured in an upcoming paper on the braincase of *Mandageria* (Ahlberg & Johanson in prep.). The palate is best preserved in F96855c, which is the basis for the description below.

In general terms, the palate compares quite closely with that of *Eusthenopteron* (Jarvik 1980, fig. 124), but there are nevertheless significant differences. As in *Eusthenopteron*, the vomers have long posterior processes and are closely sutured



**Figure 9** (a) *Mandageria fairfaxi*, F96855c, interpretative drawing of palate. (b) Palatal reconstruction of *Mandageria*. (c) Palatal reconstruction of *Eusthenopteron* (from Jarvik 1980). There are considerable differences between (b) and (c) in proportions, premaxillary morphology and dentition. Note also the presence of 'accessory vomers' in (b). Graphic conventions as in Figure 2.

to the sides of the parasphenoid. However, the parasphenoid is broader than in *Eusthenopteron* and its denticulated field is proportionately shorter; this field is also slightly convex (rather than flat or concave) in transverse section. A convex denticulated field is also characteristic of *Jarvikina* (Lebedev, pers. comm.). We have not been able to identify a buccohypophysial foramen. Anteriorly, the vomers meet in front of the parasphenoid, the intervomerine suture apparently being pierced by a canal in the usual way. Each vomer supports a fang pair and a marginal row of tiny teeth. The apical fossa is longer than in *Eusthenopteron*, and is divided in two by the previously described posterior process of the premaxilla which seems to reach (and probably fuses with) the vomer.

The palatoquadrate complex of *Mandageria* differs in several respects from that of *Eusthenopteron*. The denticulated field of the entopterygoid is proportionately shorter, barely reaching the posterior end of the vomer; the ectopterygoid and dermopalatine only suture with each other laterally, whereas their mesial laminae are separated by an exposed area of the palatoquadrate; and the marginal tooth row is missing on the anterior part of the dermopalatine. The posterior part of the palate is unfortunately not well preserved, but it seems likely that the ectopterygoid carried two pairs of fangs as in *Eusthenopteron*. The choana is poorly preserved, but seems to have been long and narrow.

Posteroventral to the vomers, but still running along the lateral edges of the parasphenoid, are narrow elongate bones, to which we assign the name 'accessory vomers' in accordance with Gardiner's (1984) terminology for actinopterygians. These bones are best observed on F98592a (Fig. 8), extending nearly to the posterior edge of the parasphenoid, but they are not very well preserved in any specimen of *Mandageria*. However, better preserved examples of the same bones are present on the second tristichopterid from Canowindra (Ahlberg & Johanson, in review) and a new large tristichopterid recently uncovered by the authors along the south coast of New South Wales. They are not known in any other sarcopterygians, and are presumably homoplastic with the accessory vomers of actinopterygians.

As can be seen, *Mandageria* has a characteristic tristichopterid palate. Some of the characteristics it shares with *Eusthenopteron* are probably tristichopterid synapomorphies, but caution should be exercised in making such judgments, given that the character states in potentially related groups are not always well known. Among other osteolepiforms, the osteolepidids *Gogonasus* (Long 1985c, 1987b) and *Medoeria* (Lebedev 1995) have vomers which overlap the anterior process of the parasphenoid from the ventral side, but lack posterior processes. A similar pattern is present in the megalichthyid *Cladarosymblema* (Fox *et al.* 1995). Outgroup comparisons with porolepiforms (Jarvik 1972) and primitive actinopterygians (Gardiner 1984) suggest that the lack of a posterior vomeral process is primitive for the Osteolepiformes. Vomers suturing in the midline anterior to the parasphenoid is a synapomorphy of the clade (Osteolepiformes [Elpistostegalia + Tetrapoda]).

Jarvik (1966, 1980, fig. 146) claims that the vomer of *Megalichthys* carries a long posterior process. However, the 'process' is in fact the subocular shelf of the ethmosphenoid, possibly overlain by the lateral edge of the parasphenoid. There is thus no reason to believe that any megalichthyid has a posterior process on the vomer. Jarvik's (1980, fig. 147) similar interpretation of *Gyroptychius milleri* can probably be dismissed on the same grounds. As far as can be determined, rhizodonts (Long 1989) also lack this process. However, the vomer of *Panderichthys* has a short posterior process which fuses to the side of the parasphenoid in the same way as in tristichopter-

ids (Vorobyeva & Schultze 1991; pers. obs. P.E.A.), so this character could be a tristichopterid–elpistostegid synapomorphy. This topic will be addressed further by the authors in a later paper. The divided apical fossa seems to be a synapomorphy of *Mandageria* and *Eusthenodon* (see Section 2.1.2.), while the transversely convex denticulated field of the parasphenoid is probably an autapomorphy of *Mandageria*.

**2.1.12. Mandible.** In *Mandageria fairfaxi*, the external surface of the mandible can be observed in certain specimens (F96508, F96857), but only a portion of the internal surface of the mandible can be observed in F96855d (Figs 11b, 12b). As observed on F96857 and F96855d, the anteriomost portion of the mandible possesses a well developed fang pair. Among tristichopterids, this fang pair is present in *Eusthenodon* (Jarvik 1952, fig. 49), *Platycephalichthys* (Vorobyeva 1977, pl. XIV), and the second tristichopterid from Canowindra (Ahlberg & Johanson, in review). However, it also occurs in the megalichthyids *Megalichthys* (Thomson 1962, pl. 1; Jarvik 1966, fig. 6), *Cladarosymblema* (Fox *et al.* 1995, figs 46–50) and *Ectosteorhachis* (Fox *et al.* 1995, fig. 53), in the rhizodonts *Notorhizodon* (Young *et al.* 1992), *Barameda* (Long 1989) and *Rhizodus* (pers. obs. P.E.A.), in *Panderichthys* (Gross 1941) and all known Devonian tetrapods (*Ichthyostega*, Jarvik 1980; *Acanthostega* pers. comm., J. A. Clack; *Ventastega*, Ahlberg *et al.* 1994; *Elginerpeton* and *Obrucherichthys* Ahlberg 1995) and in the osteolepidids *Thysanolepis* (Vorobyeva 1977, fig. 36) and *Vorobjewia* (Young *et al.* 1992, fig. 18). By contrast, it is absent in the tristichopterids *Eusthenopteron* and *Jarvikina* (Jarvik 1980; Vorobyeva 1977; pers. obs. P.E.A.), and in many osteolepidids. The significance of this character distribution needs to be investigated further.

Internal (i.e. posteromesial) to the anterior part of the dentary lies a deep precoronoid fossa, partly covered with displaced material from the upper jaw in F98655d (Figs 11b, 12b); this fossa in turn is bounded mesially by a prominent rib formed from the mesial lamina of the splenial bone together with the anterior end of the prearticular. The anterior end of the rib rises into a distinct process which forms the support for the parasymphyseal plate; the processes off the left and right jaw rami are in intimate contact. The parasymphyseal plate itself is not readily visible. There may be a partial parasymphyseal plate on the right parasymphyseal process, but this area is damaged and partially overlain by material from the upper jaw. Despite the incompleteness of the specimen, it is clear from the shape of the supporting process and surrounding bones that the parasymphyseal plate was small and failed to contact the anterior coronoid.

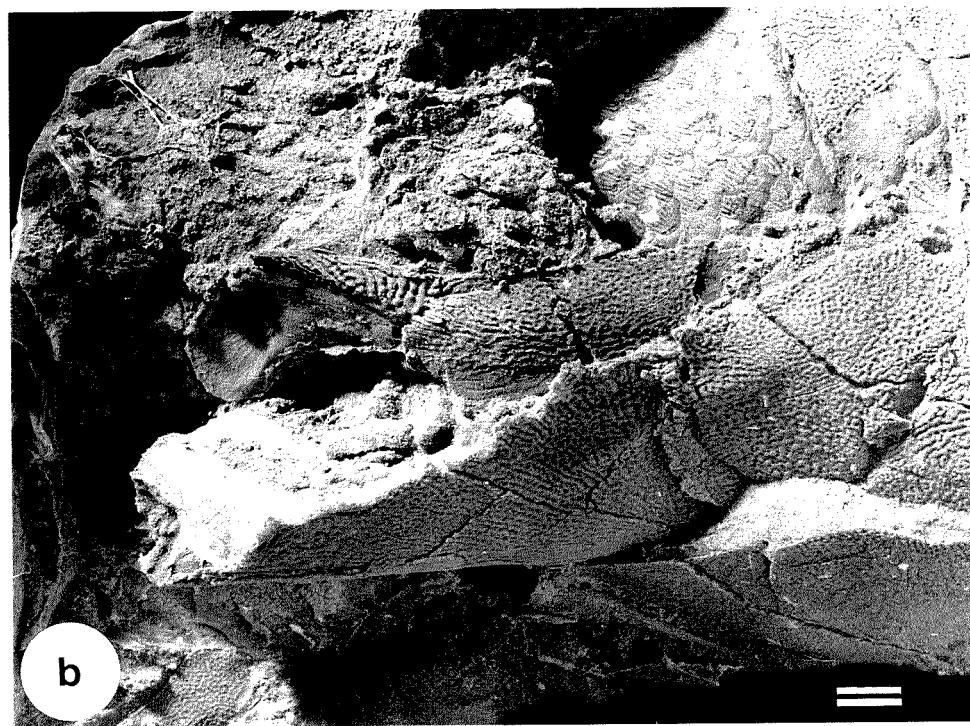
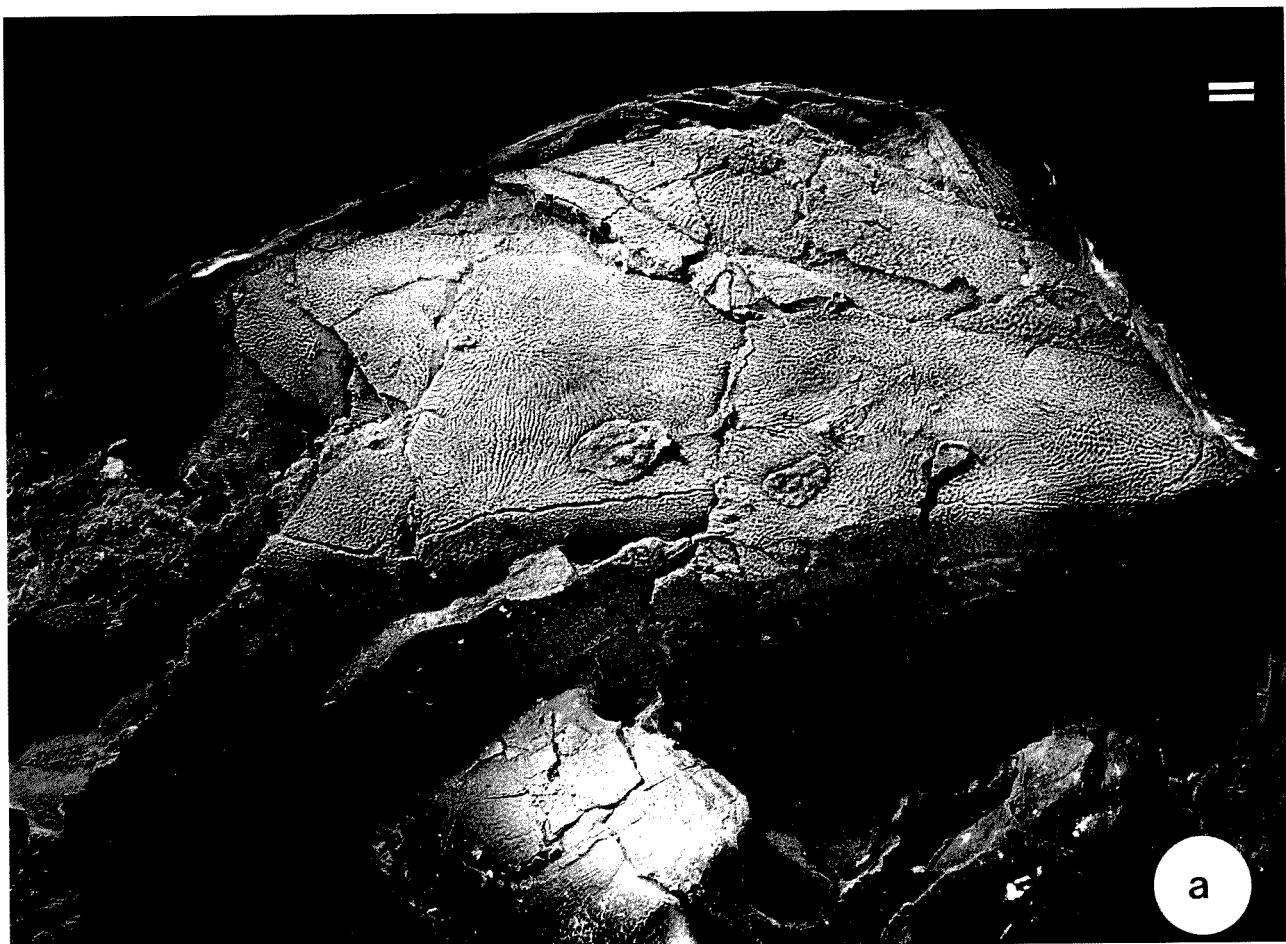
This conforms to what Jarvik (1980, fig. 143B) calls the 'rhizodontid' ('rhizodontid' sensu Jarvik = tristichopterid, this paper), which seems to be universal for tristichopterids. It also occurs in *Panderichthys* (Vorobyeva 1962) and in the rhizodont (sensu stricto) *Notorhizodon* (Young *et al.* 1992, fig. 33). By contrast, osteolepidids such as *Medoeria* (Lebedev 1995) and *Gogonasus* (Long 1987b; Fox *et al.* 1995) have an elongated and rather large parasymphyseal plate which contacts the anterior coronoid.

The coronoid morphology of *Mandageria* seems to compare well with that of *Eusthenopteron*, although the preservation in F96855d is patchy. However, one interesting difference presents itself; unlike in *Eusthenopteron*, there are no marginal coronoid teeth (Figs 11b, 12b), except on the posterior part of the posterior coronoid. This condition is matched in *Eusthenodon wängsöji* (BMNH P64121) and in the second tristichopterid from Canowindra.

**2.1.13. Branchial arches.** The basibranchial skeleton, up to and including ceratobranchials and ceratohyals, is almost perfectly preserved in F98593b (Figs 13a, b); less complete but

still informative gill skeletons are present in F96855d and F98592b. These specimens make an interesting comparison with Jarvik's (1954, 1980) reconstruction of the branchial skeleton in *Eusthenopteron*. Before going into this comparison,

two further aspects of branchial preservation in *Mandageria* should be mentioned. Firstly, part of the hyomandibula is preserved in association with the braincase in F98593a; secondly, the 'steinkern' filling the head in F98721 shows clear



**Figure 10** *Mandageria fairfaxi*, F96855a. (a) Skull and pectoral girdle in dorsal view. (b) Closeup of pectoral girdle. (c, d, facing page). (c) Interpretative drawing of (a). (d) Interpretative drawing of (b). Graphic conventions as in Figure 2.

impressions of large gill rays, which closely resemble those in *Eusthenopteron* (Jarvik 1980, fig. 144B). As mentioned above, these features will be described with the braincase in a forthcoming paper.

The ventral midline of the branchial skeleton is formed from two basibranchials, the anterior element being the larger. A structure in the midline anterior to the gill skeleton is probably the sublingual rod, and a urohyal much like that of *Eusthenopteron* can be seen lying slightly displaced beneath the right branchial arches in F98593b. The anterior basi-

branchial supports, from anterior to posterior, the hypohyals, first and second arch hypobranchials, and the posterior basibranchial. This is exactly as in *Eusthenopteron*, and the morphology of the elements is also strikingly similar. The dorsal surface of the anterior basibranchial carries a single bilobed denticulated plate in F98593b, but a pair of narrower plates are present in F98592b; the latter pattern matches Jarvik's reconstruction of *Eusthenopteron*. The denticulated plates on the hypobranchials and ceratobranchials also resemble those of *Eusthenopteron* in all essentials.

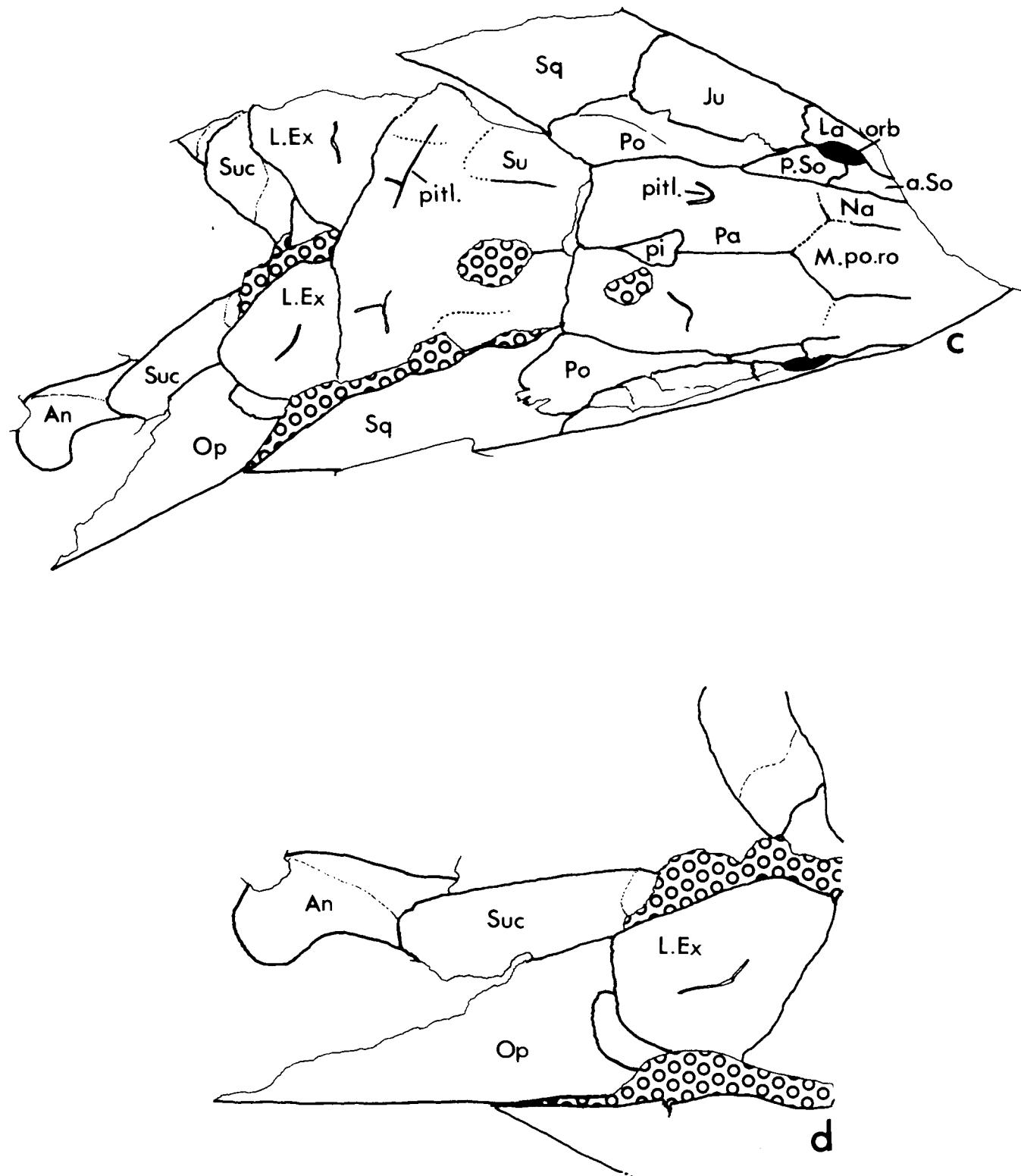
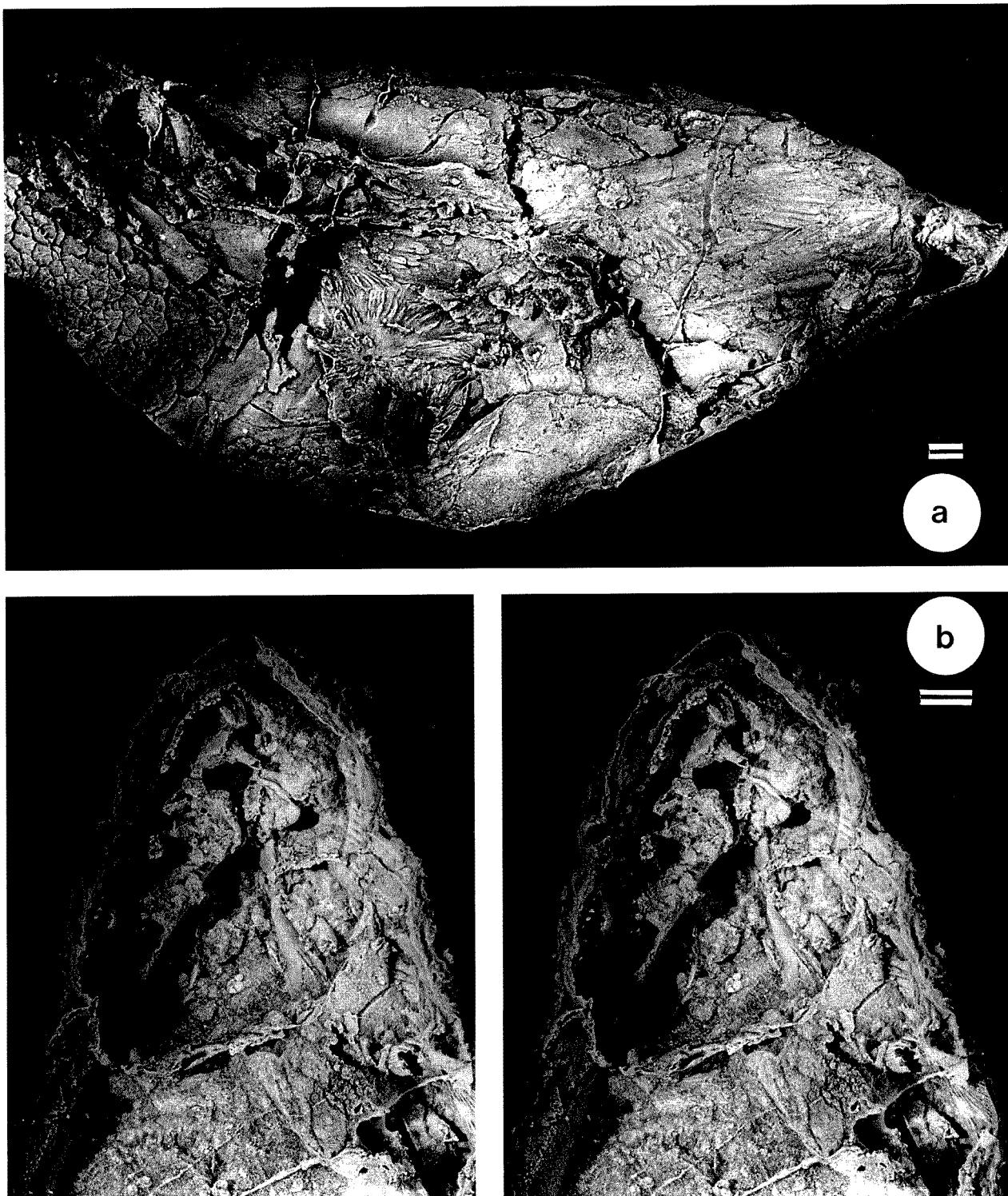


Figure 10 (continued)



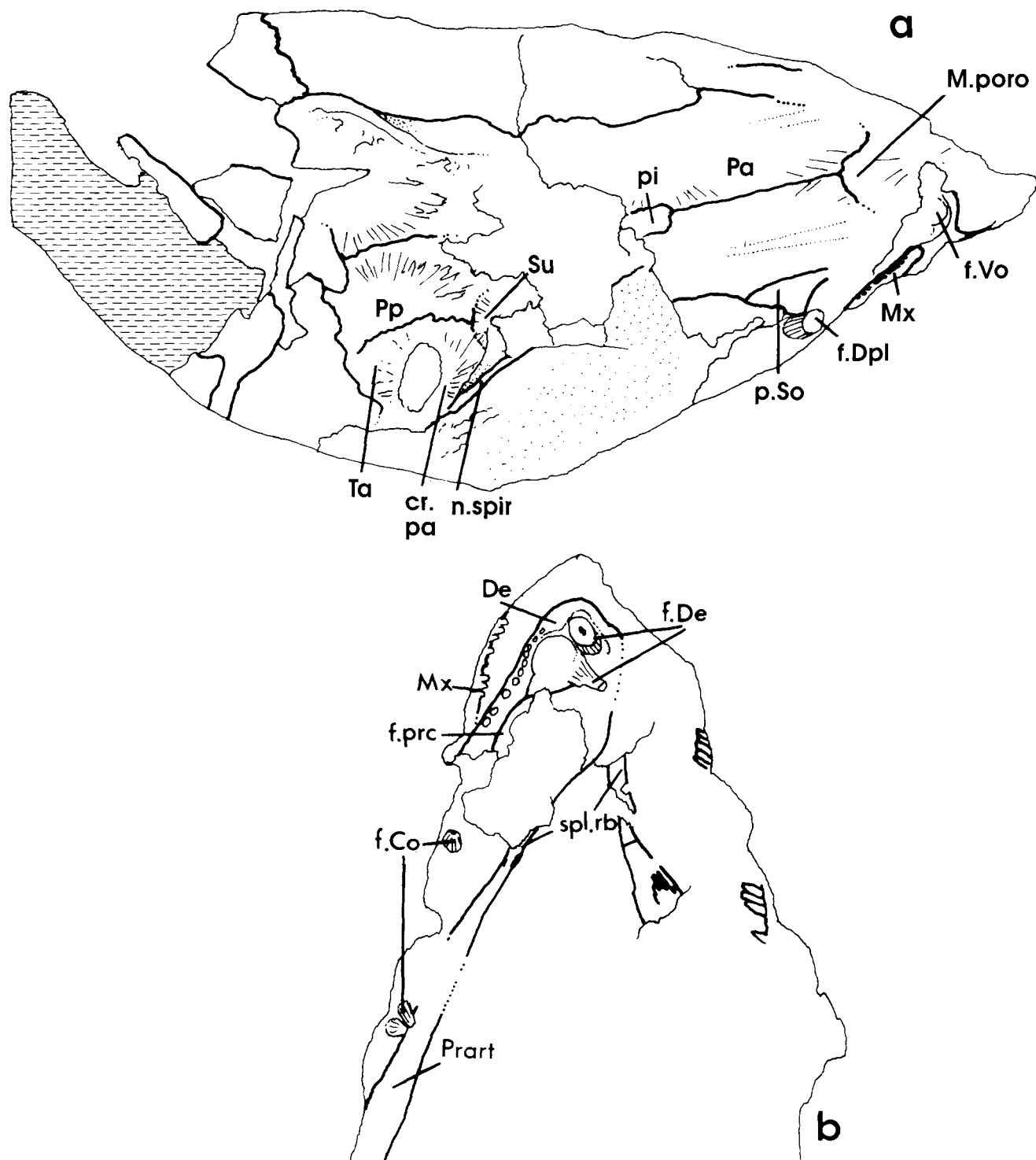
**Figure 11** *Mandageria fairfaxi*. (a) F96855b, bones of skull roof, internal view. (b) F96855d, anterior half of lower jaws surrounded by parts of upper jaws. Note the strongly developed fang pair at the anterior end of the dentary.

The posterior basibranchial is a short, trapezoidal element. The posterior margin of this bone, which is well preserved, consists of two articular facets for the third arch hypobranchials; the facets meet in the midline, and there was certainly neither a posterior extension of this bone, nor a separate third basibranchial. On the left side of F98593b, the fourth arch hypobranchial can be seen to articulate with the posteroventral surface of the third arch basibranchial approximately halfway along the length of the latter.

The posterior part of the basibranchial skeleton differs strikingly from Jarvik's (1954, 1980) reconstruction. In the

latter (Jarvik 1980, fig. 113), the posterior basibranchial is reconstructed as a long element supporting the fourth arch hypobranchial directly. However, it is interesting to note that the boundary between preserved and reconstructed structure, as indicated by the shading of the figure, coincides exactly with the real posterior end of the basibranchial in *Mandageria*.

Among other early sarcopterygians, the basibranchial skeleton has been described in the osteolepiform *Medoevia* (Lebedev 1995), the porolepiform *Glyptolepis* (Jarvik 1972) and the lungfish *Griphognathus* (both, Miles 1977). In *Medoevia*, the proportions of the basibranchials are somewhat

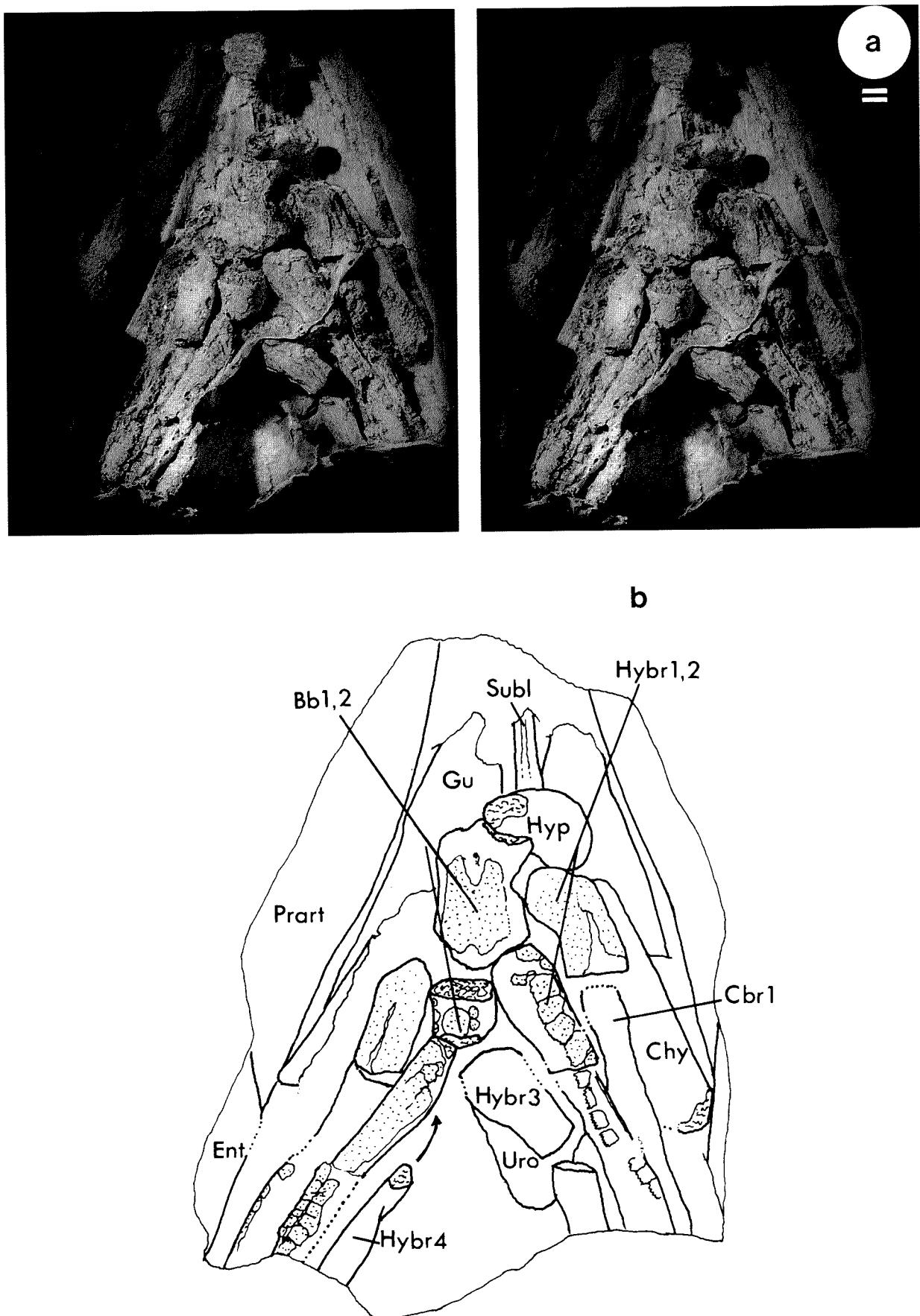


**Figure 12.** *Mandageria farfaxi*. Interpretative drawings of photographs in Figure 11. (a) F96855b. (b) F96855d.  
Graphic conventions as in Figure 2.

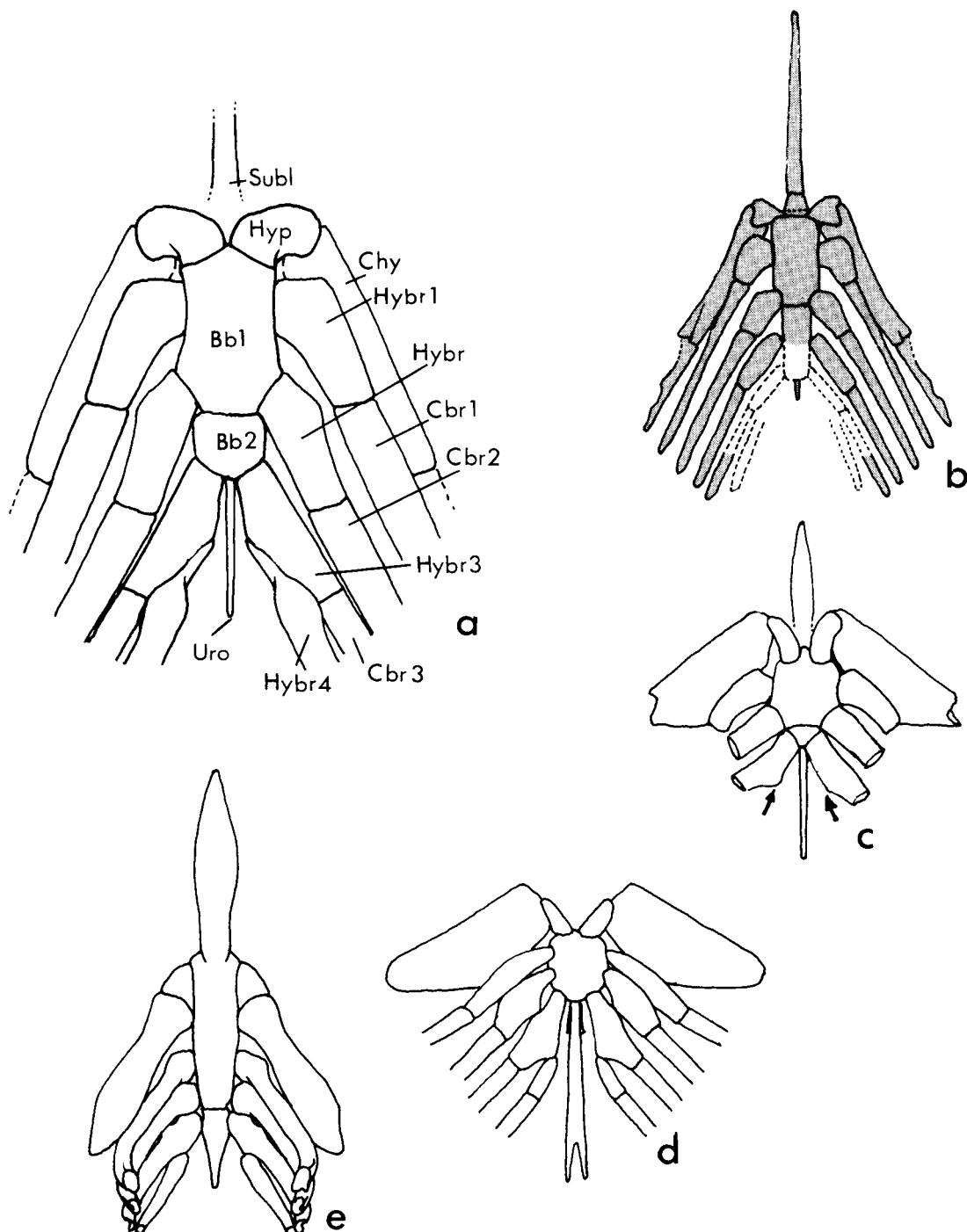
different from those in *Mandageria*, being broader and more rounded, but the construction is exactly the same. The posterior basibranchial only carries the third arch hypobranchials, but the articular facets for the fourth arch can be seen on the posteroventral surfaces of the latter (Lebedev 1995, fig. 18). *Glyptolepis* differs from osteolepiformes in having only one basibranchial. However, this basibranchial carries hypobranchials one to three, with four supported by three as described above. It thus seems clear that the one basibranchial of *Glyptolepis* corresponds to both basibranchials in *Mandageria* or *Medoevia*, and that the arrangement of the basibranchials is fundamentally the same in all three genera. The lungfish

*Griffognathus* (Miles 1977, fig. 137; Campbell & Barwick 1987, fig. 6a, 7) again has two basibranchials, the anterior one possibly incorporating a sublingual rod, and the basibranchial pattern is again the same as in *Mandageria*. The living coelacanth *Latimeria* has a single basibranchial supporting basibranchials one to three, with four being carried by three (Millot & Anthony 1958, pl. XLVI).

It should be clear from the above that the branchial pattern of *Mandageria* matches that in all other known Devonian sarcopterygians, but differs from Jarvik's reconstruction of *Eusthenopteron* (Fig. 14). In light of this, and in particular the correspondence between the full extent of the posterior



**Figure 13** *Mandageria fairfuxi*, F98593b. (a) Basibranchial skeleton in dorsal view, stereo pair. (b) Interpretative drawing of (a). Graphic conventions as in Figure 2.



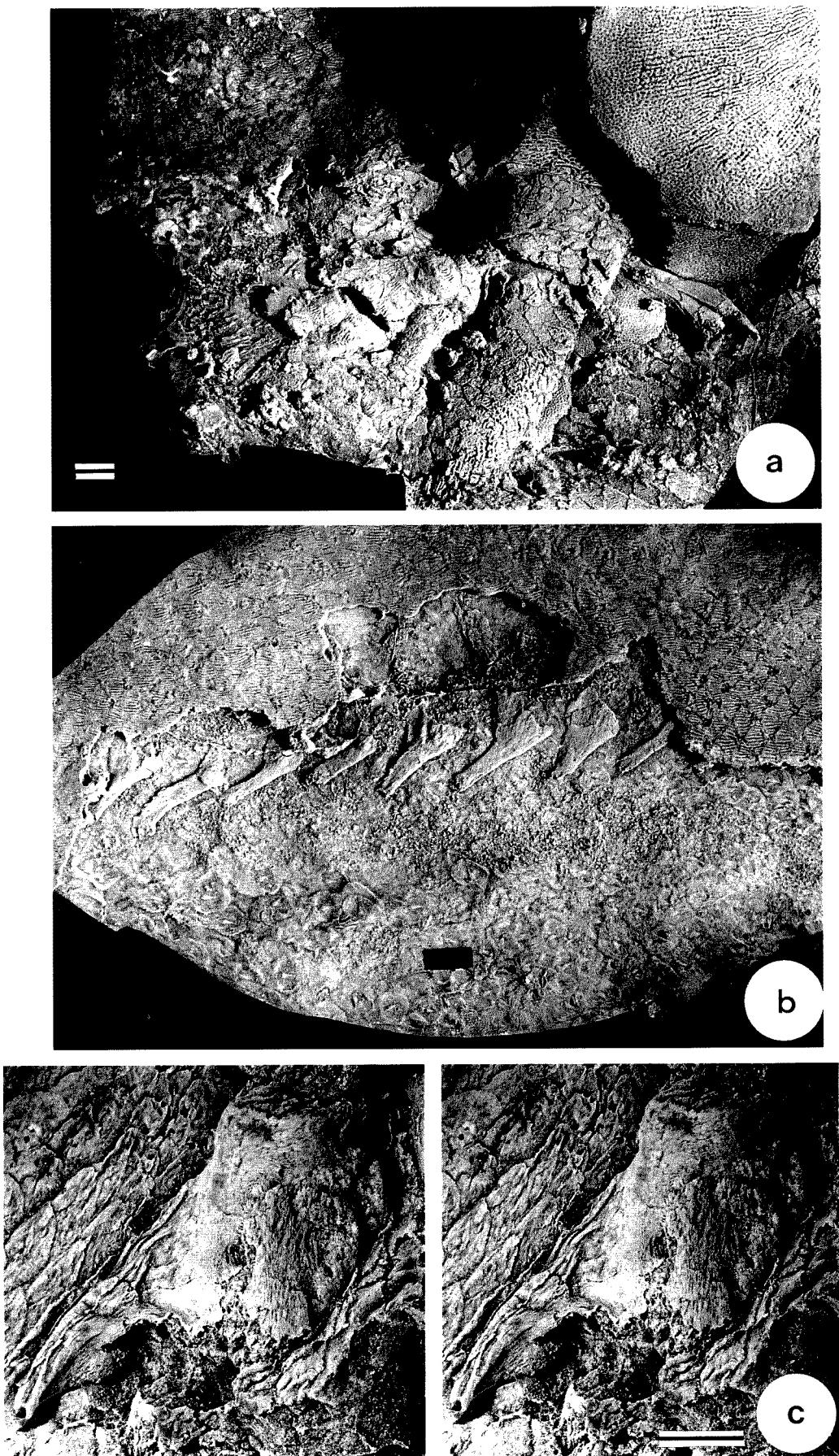
**Figure 14** Basibranchial skeletons. (a) Reconstruction of *Mandageria fairfaxi*. (b) Jarvik's (1980) reconstruction of *Eusthenopteron*. Note that the preserved part (shaded) corresponds to the basibranchial skeleton of *Mandageria*, but that the reconstructed parts have no counterparts in the latter genus. Graphic conventions as in Figure 2. (c) The osteolepidid *Medoevia* (Lebedev 1995). (d) The porolepiform *Glyptolepis* (Jarvik 1972). (e) The lungfish *Griphognathus* (Miles 1977). (c–e) agree with *Mandageria* in the arrangement of the gill arches.

hypobranchial in *Mandageria* and the ‘preserved part’ of this element in Jarvik’s reconstruction, we conclude that *Eusthenopteron* actually has a basibranchial skeleton similar to *Mandageria fairfaxi*. Furthermore, we conclude that the articulation of the fourth hypobranchial with the third hypobranchial, rather than with a basibranchial, is the primitive condition for the Dipnomorpha + Tetrapodomorpha clade within the Sarcopterygii (Ahlberg 1991).

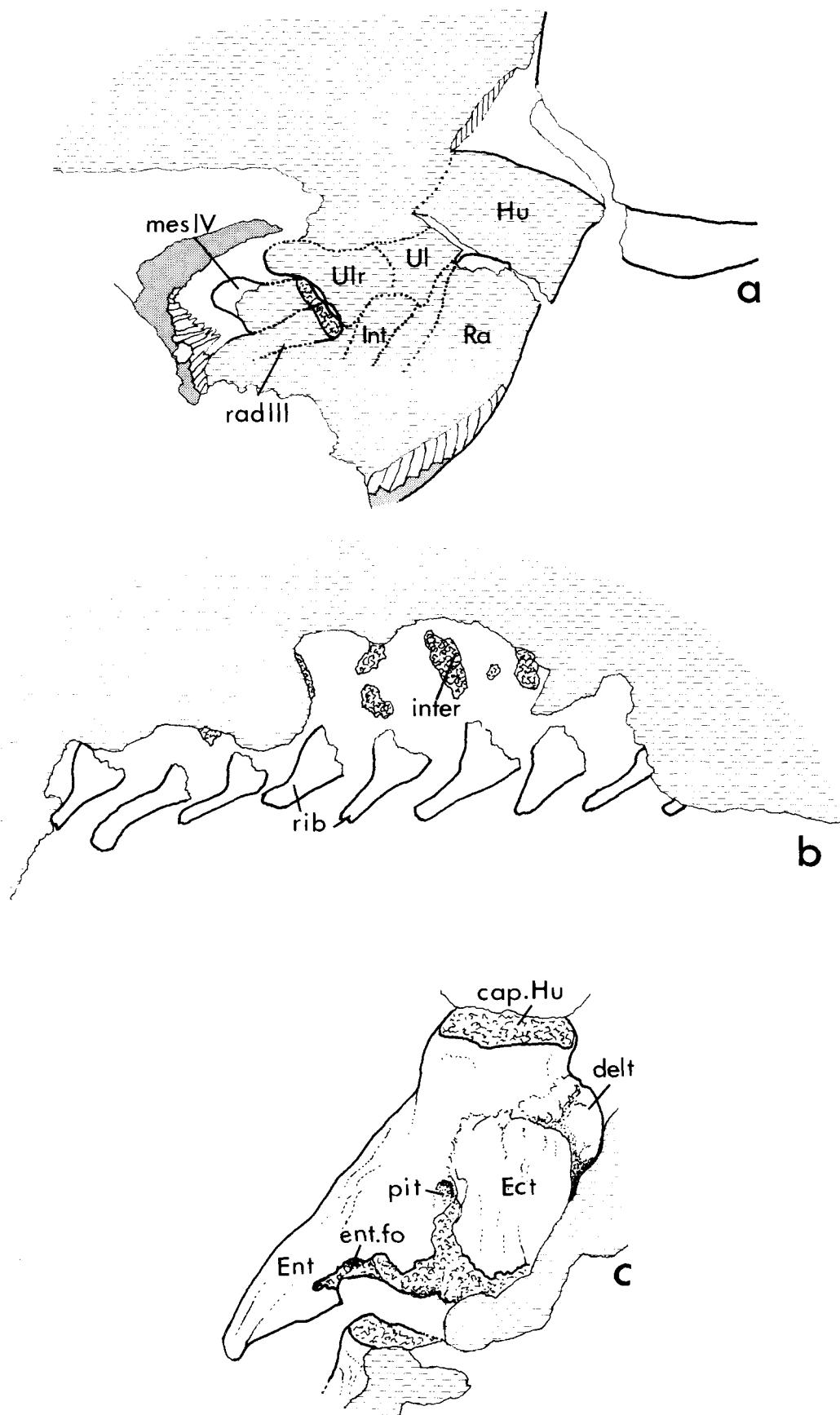
## 2.2. Postcranial skeleton

**2.2.1. Pectoral girdle.** The shoulder girdle is partially preserved in a number of specimens, notably F96508 (Fig. 15a)

and F96855 (Figs 10a, b) which between them show almost the complete structure. The girdle contains the usual osteolepidiform complement of bones: posttemporal, supracleithrum, anocleithrum, cleithrum, scapulocoracoid and clavicle. It is not clear whether an interclavicle is present. Overall, the general resemblance to *Eusthenopteron* is rather close. Of the dorsal pectoral girdle bones, the posttemporal is the least well known. In F96508 both posttemporals remain in position, posteromesial to the lateral extrascapulars, but are largely covered by matrix. In F96855 (Fig. 10a, c), the left posttemporal can be seen fairly clearly; it is similar to an extrascapular in shape, but smaller, and has a large anterior overlap area for the median extrascapular. The supracleithrum and



**Figure 15** *Mandageria fairfaxi*. (a) F96897a. Bones of right pectoral fin in dorsolateral view. (b) F96897b, trunk vertebrae and ribs in dorsal view. There appear to be four scale rows per vertebral length (and thus per body segment). (c) F96895, right humerus, stereo pair in dorsal view.



**Figure 16** *Mandageria fairfaxi*. Interpretative drawings of photographs in Figure 15. (a) F96897a. (b) F96897b. (c) F96895. Graphic conventions as in Figure 2.

anocleithrum are preserved in articulation in both specimens. The proportions of these bones differ from those in *Eusthenopteron*. The exposed and ornamented area of the supracleithrum is longer in *Mandageria*, whereas the orna-

mented part of the anocleithrum is substantially shorter and triangular rather than four-sided. The supracleithrum would almost touch the anterodorsal corner of the cleithrum when the girdle was assembled, leaving the anocleithrum visible as

a broad wedge-shaped element posterior to this junction (Fig. 10). Ventral to the ornamented area, the anocleithrum is developed into a broad, curving process which forms the overlap area for the cleithrum. This process can also be observed in *Medoeria* (Lebedev 1995), *Eusthenopteron* (Jarvik 1980) and *Canowindra* (Long 1985a) though it differs somewhat in proportions and orientation from genus to genus; it is presumably a generalised osteolepiform feature.

The cleithrum and clavicle correspond in all essentials to those of *Eusthenopteron*. The scapulocoracoid is not well exposed on any specimen. However, in F96895 the robust dorsal buttress and approximately triangular body of the bone, poorly preserved, can be seen in dorsomedial view. It appears to have the usual osteolepiform tripodal structure.

**2.2.2. Pectoral fin.** The pectoral fin of *Mandageria fairfaxi* is preserved in four specimens (F96508, F96861, F96895, F96897a). On F96895 (Figs 15c, 16c), the scales have been stripped from the dorsomedial surface of the basal lobe revealing a well preserved humerus in articulation with scapulocoracoid (see above) and ulna.

In overall shape and relative size, the pectoral fin of *Mandageria* is almost identical to that of *Eusthenopteron*. Furthermore, the endoskeleton of the fin (Figs 15a, 16a) has exactly the same structure as in *Eusthenopteron* (Andrews & Westoll 1970a; Jarvik 1980). The differences between the two are almost wholly confined to the humeral morphology.

As in *Eusthenopteron*, the humerus (Figs 15c, 16c) can be described as a cylindrical body carrying a number of processes. The proximal articular surface, the caput humeri, is gently convex and not very differentiated in *Mandageria*. This matches the condition in *Eusthenopteron* and in those osteolepidids whose humeri have been described (*Sterropterygion*, Rackoff 1980; *Beelarongia* Long 1987a; *Medoeria* Lebedev 1995), but differs from the rhizodont condition where a large bulbous caput humeri is offset from the rest of the humerus by a distinct neck (Andrews & Westoll 1970b; Long 1989). Outgroup comparison with other sarcopterygians shows that the rhizodont condition is derived.

The most prominent feature of the humerus is the entepicondyle, which is large and distinct, and is separated from the main body of the humerus on the postaxial side by a shallow valley. In *Eusthenopteron* (and other known osteolepiforms), the entepicondyle is pierced by a short canal known as the entepicondylar foramen, which carried the ulnar nerve and blood vessels (Andrews & Westoll, 1970a, p. 246). The proximal opening lies just where the anterior margin of the entepicondyle merges with the body of the humerus, while the distal opening is on the distal surface of the humerus between the entepicondylar process and the ulnar articulation. If the humerus of *Eusthenopteron* (exemplified by BMNH P60388) is viewed from the same angle as the *Mandageria* humerus of F96895 (i.e. in dorsomedial view), the proximal end of the entepicondylar foramen on *Eusthenopteron* is clearly visible. However, in F96895, the foramen cannot be seen; we presume that it occupies a more ventral position on the entepicondyle. At the distal end of the humerus, a depressed area of unfinished bone extends from the ulnar facet onto the entepicondyle. This area appears to house the distal opening of the entepicondylar foramen, although the preservation is imperfect. The mesial end of the depressed area forms a distinct notch in the margin of the entepicondyle, which would grip the edge of the ulna in life. This notch seems to correspond to the humeral process of Andrews & Westoll (1970a, fig. 10) although it is less distinct. The ventral face of the humerus is concealed in F96895; however, the slightly collapsed latex peel of the ventral surface of F96508 (from an *in situ* slab which was subsequently reburied to prevent vandalism) seems to show

the generalised osteolepiform pattern of a 'humeral ridge' (Andrews & Westoll 1970a) running along the ventral face of the entepicondyle and diagonally across the body of the humerus.

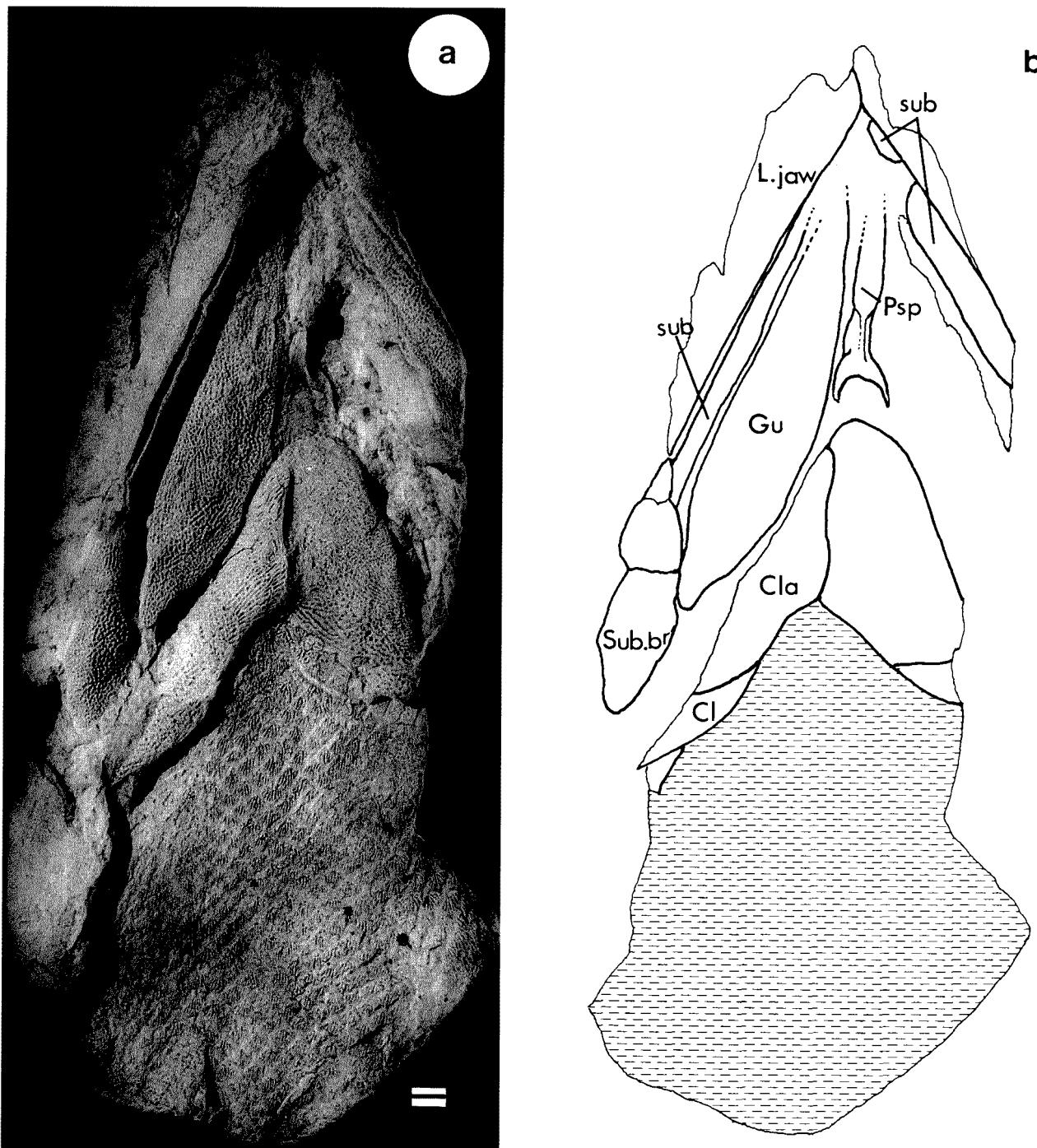
The ectepicondyle of *Mandageria fairfaxi* is very distinctive. It occupies a much larger area than the corresponding process in *Eusthenopteron*, but is also much flatter; its broad 'apex' is in fact faintly concave. However, there is no indication of postmortem compression of this area or of the humerus as a whole. Midway along the postaxial margin of the ectepicondyle is a conspicuous pit, which may house a foramen. There is only a shallow notch in the corresponding position on *Eusthenopteron* (pers. obs. by P.E.A. of BMNH P60388). A narrow strip of rough bone runs from this pit to the distal end of the humerus.

A smaller oblong process is visible anterior and preaxial to the ectepicondyle. Comparison with *Eusthenopteron* suggests that this is the deltoid process. If this interpretation is correct, the supinator process is concealed under a patch of squamation at the preaxial margin of the bone.

Although the humeral morphology of *Mandageria* differs somewhat from that of *Eusthenopteron*, the two are nevertheless comparable. By contrast, the humeri of rhizodonts (Andrews & Westoll 1970b; Long 1989), *Panderichthys* (Vorobyeva & Kuznetsov 1992), and basal tetrapods (Jarvik 1980, fig. 166; Coates & Clack 1990) all differ strongly from that of *Mandageria*. As regards osteolepidids, *Sterropterygion* (Rackoff 1980), *Rhizodopsis* (Andrews & Westoll 1970b) and *Beelarongia* (Long 1987a) seem to have broader and more flattened humeri than *Mandageria*, while the humerus of *Medoeria* appears somewhat more similar to *Mandageria*, but is too incomplete to be fully interpreted. Overall, *Mandageria* has a *Eusthenopteron*-like humerus; the differences (position of entepicondylar foramen, large flattened ectepicondyle, pit/foramen on postaxial margin of the ectepicondyle) are more likely autapomorphies of *Mandageria* than synapomorphies shared with other taxa. These skeletal autapomorphies presumably reflect unique features of the muscle arrangement, and hence subtle differences in functional morphology compared to *Eusthenopteron*.

The ulna is a short and stout bone (Figs 15a, 16a), as in *Eusthenopteron* (Andrews & Westoll 1970a, fig. 13g–m), with a flat articular surface proximally, and two facets distally for the ulnare and intermedium. The radius, which is preserved in F96861, F96896 and F96897, appears exceedingly robust. However, on F96896, part of the scale covering of the radius is broken away, and it can be seen that the radius had similar proportions to *Eusthenopteron*; it is the covering scales which are thickened, giving the impression of robustness. These scales are not only thick, but are covered with a coarse and distinctive ornament not seen elsewhere on the body (see also F96897a, Figs 15a, 16a). It seems probable that the scales served to create a rigid and hydrodynamically efficient leading edge to the pectoral fin; it is interesting to speculate whether the function of the unique ornament was likewise hydrodynamic, or whether it served as protection against abrasion. The ulnare and fourth axial mesomere carry broad postaxial processes like those of *Eusthenopteron* and *Rhizodopsis* (Andrews & Westoll 1970a, b).

**2.2.3. Posterior fins.** Several specimens, including F96508, F96903 (Figs 18a, 19a) and F96899 (Figs 18b, 19b) preserve some of the more posterior body fins. They give a reasonably clear picture of the caudal, anal and pelvic fins, but the two dorsal fins are unknown. The caudal fin is diphycercal, with the hypochordal lobe very slightly larger than the epichordal. The internal skeleton, partly exposed in F96899, appears identical to that of *Eusthenopteron*. Unfortunately, the thin

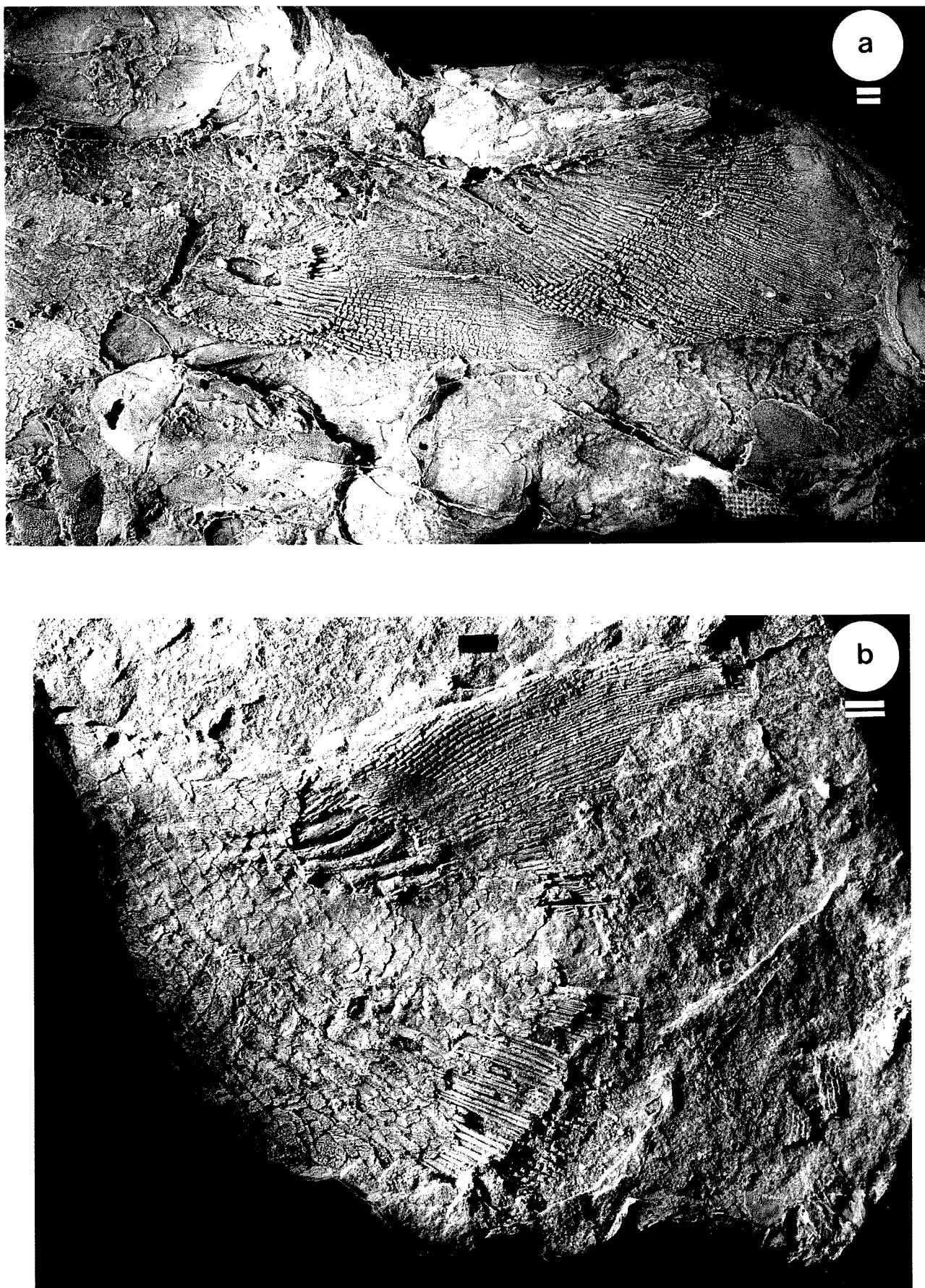


**Figure 17** *Mandageria fairfaxyi*, F98594, lower jaw, gular series, and anterior body scales in ventral view: (a) photograph, (b) interpretative drawing. Graphic conventions as in Figure 2.

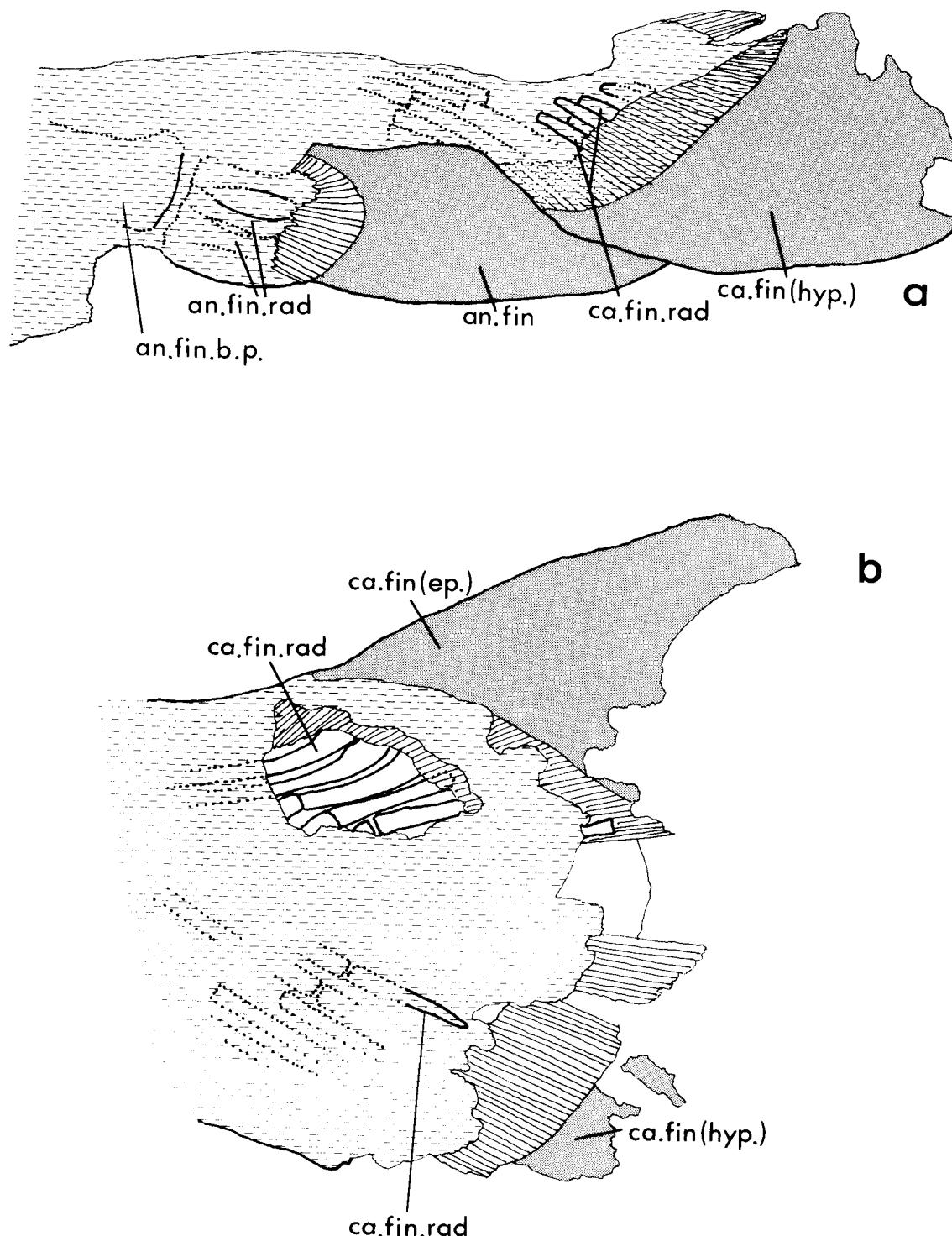
distal parts of the fin web are not well preserved. However, it appears that the tail was not as obviously three-lobed (trityceral) as in *Eusthenopteron*, and it also seems to have a low aspect ratio (dorsovenital length of fin/antero/posterior width of fin), with a deep caudal peduncle. The anal fin again resembles that of *Eusthenopteron*, and the same appears to be true for the pelvic fins although the latter are not well preserved. However, the relative positions and sizes of these fins differ substantially from the *Eusthenopteron* morphology (Fig. 23). The caudal fin is strikingly small (this is obvious in the more complete specimens even prior to reconstruction), and the anal and pelvic fins are placed much closer to the tail. These differences must have had a substantial impact on the swimming performance of *Mandageria*.

Most Devonian lobe-finned fishes are characterised by low

aspect ratio tails, deep caudal peduncle and posteriorly placed median fins, suggesting that they were ‘unsteady swimmers’ (Webb 1982; Ahlberg 1992) with good powers of acceleration but a poor capacity for sustained swimming. *Eusthenopteron* actually shows these traits to a lesser degree than many osteolepiforms; its tail, posterior dorsal and anal fins all have relatively high aspect ratios, and the former is separated from the two latter by a fairly long and narrow caudal peduncle (Jarvik 1980, fig. 72). All this suggests that *Eusthenopteron* was a reasonably able sustained swimmer. In *Mandageria*, however, the low aspect ratio tail, deeper caudal peduncle, and posteriorly placed anal fin suggest that the capacity for sustained tail-propelled swimming was extremely poor. The small size of these fins supports this conclusion. It seems likely that *Mandageria* used ‘normal’ tail-propelled swimming, driven



**Figure 18** *Mandageria fairfaxi*. (a) F96903, ventral lobe of caudal fin and anal fin, lateral view. (b) F96899, partial caudal fin, lateral view.



**Figure 19** *Mandageria fairfaxi*. Interpretative drawings of Figure 18. (a) F96903. (b) F96899. Graphic conventions as in Figure 2.

by body undulations, exclusively for bursts of acceleration; slow swimming was probably accomplished by paddling or undulating movements from the paired and median fins, as in *Esox* or *Lepisosteus* (pers. obs. P.E.A.). Indeed *Mandageria* must in life have appeared not unlike a large garpike, probably spending a great deal of its time motionless or nearly motionless in the water. It is interesting to note that at least two of the other sarcopterygians from Canowindra show similar or even more extreme locomotory adaptations. This will be discussed more fully in a subsequent paper.

**2.2.4. Vertebral column.** At least two types of vertebral column are known among the Tristichopteridae. *Eusthenopteron* (Andrews & Westoll 1970a; Jarvik 1952, 1980)

has rhachitomous vertebrae similar to those of many early tetrapods; the intercentra are large and crescentic, while the pleurocentra are small and dorsal in position. This pattern also occurs in the earlier and apparently more primitive genus *Tristichopterus* (Andrews & Westoll 1970b). *Eusthenodon*, on the other hand, has complete ring-centra (Lebedev, pers. comm.; Ahlberg & Trewin 1995). Outgroup comparison with other osteichthyans (Andrews & Westoll 1970b; Gardiner 1984; Ahlberg & Trewin 1995) suggests that the condition in *Eusthenopteron* is primitive.

The vertebral column of *Mandageria* is faintly visible through the squamation in many specimens, but is difficult to interpret. However, it never shows any trace of ring centra.

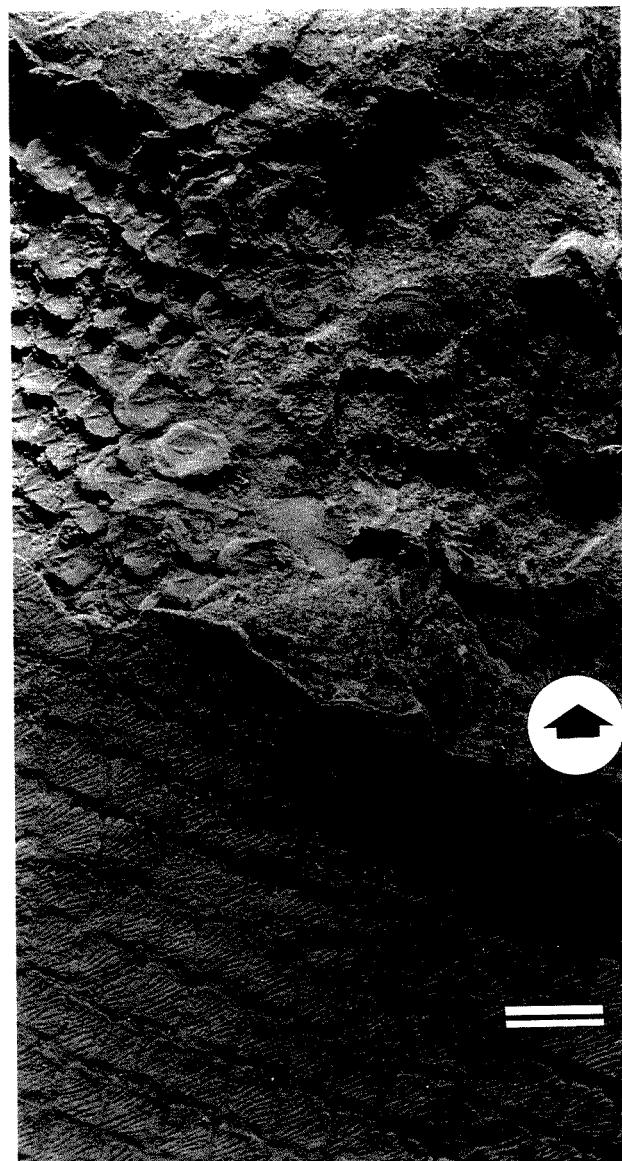
Only in one specimen, F96897b, has a thin sheet of sand entered the body cavity and produced a detailed mould of part of the thoracic backbone (Figs 15b, 16b). This specimen shows two sets of structures: shapeless blobs of unfinished bone which may represent centra, and a row of better ossified, rod-like, proximally expanded elements. It is difficult to determine the orientation of this vertebral column fragment: the fish is flattened obliquely, so the vertebral column could be preserved in either dorsal or lateral view. However, comparison with *Eusthenopteron* (Jarvik 1980, fig. 95) shows that the rod-like bones are ribs rather than neural arches. This indicates that we are seeing part of the right side of the vertebral column in dorsal view, and that the shapeless patches of unfinished bone represent the internal faces of intercentra. Curiously, there is no trace of the dorsal components of the vertebral column such as the neural arches. The most probable explanation is that sand only filled part of the body cavity, and failed to mould the more dorsal elements. It is also possible that decomposition of the notochord caused the dorsal part of the column to be lifted off and deposited somewhere else in the body cavity where there was no sand. On the whole the vertebral column of *Mandageria* is very poorly ossified, and probably consists of small separate centra around a persistent notochord.

**2.2.5. Scales.** One of the most striking features of *Mandageria* is the very small size of the scales. Although we have not been able to make a precise count, we estimate that the body would carry approximately 120 scale rows between the shoulder girdle and the caudal peduncle. Scale rows in osteichthians are segmentally derived structures, and the number of scale rows per body segment is always an integer. *Eusthenopteron* has around 50 scale rows (Jarvik 1980), so, given that *Eusthenopteron* seems to have one scale row per body segment (same number of vertebrae as scale rows; Jarvik 1980), it might appear likely that *Mandageria* has two rows per body segment. However, F96897b seems to show four scale rows per vertebral length (Fig. 15). Whatever the case, the increased number of scale rows is certainly an autapomorphy. The scales are in other respects of normal tristichopterid pattern. They are basically round, although the exposed ornamented area often has a distinct posterior corner and is sometimes offset by a ‘waist’ from the anterior unornamented part of the scale (Fig. 20). There is an oblong boss in the middle of the internal face. Other than at the leading edges of the pectoral fins (see above) the scale ornament is rather fine and consists of anteroposterior, subparallel, slightly undulating grooves. There are no denticles nor any trace of cosmine anywhere on the dermal bones. We have not been able to identify basal scutes either on the median or the paired fins.

### 3. Discussion and conclusions

*Mandageria fairfaxi* is strictly speaking the second member of the Tristichopteridae described from Australia, after *Marsdenichthys longioccipitus* (Long 1985b). However, this latter taxon may in fact be referable to the Rhizodopsidae (Long, pers. comm.). A second tristichopterid from Canowindra is described in an upcoming paper (Ahlberg & Johanson, in review).

Until now, the tristichopterids have appeared to be largely if not exclusively restricted to the Euramerican continents. *Tristichopterus*, the oldest known member, comes from the Givetian of Scotland (Egerton 1861). Frasnian members include *Eusthenopteron* from Europe and North America, and *Jarvikina* and *Platycephalichthys* from western Russia and Latvia (Vorobyeva 1962, 1977). In the Famennian, *Eusthenodon* is recorded from East Greenland (Jarvik 1952) and central

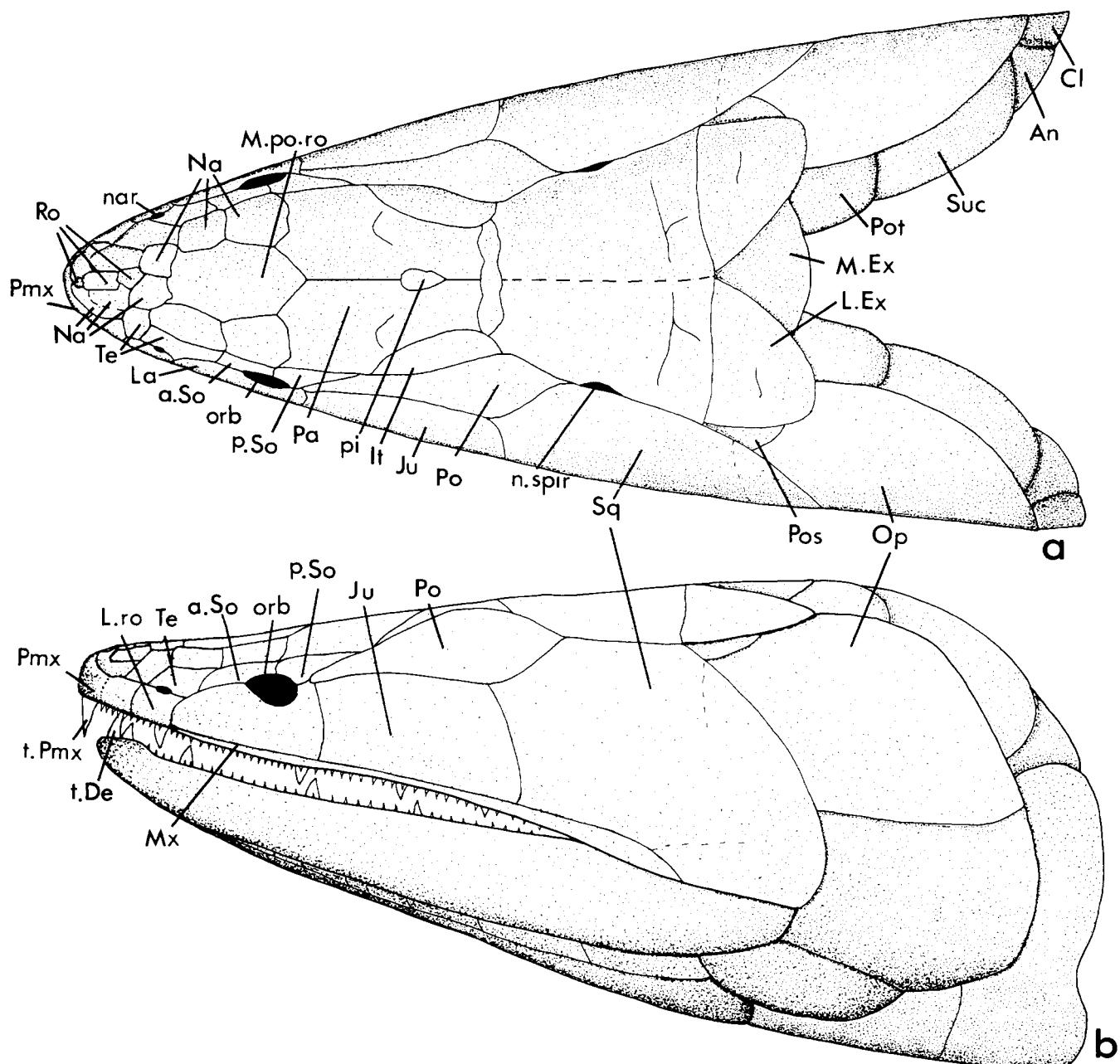


**Figure 20** *Mandageria fairfaxi*, F98720. Body scales in external and internal view. Arrow indicates individual scales showing ‘waisting’, as described in text.

Russia (Alexeev *et al.* 1994), while the probable tristichopterid *Hyneria* Thomson, 1968 occurs in the Catskill Formation of the USA. By contrast, the only tristichopterid records from Gondwana (other than *Marsdenichthys*) were some isolated bones from Grenfell, NSW, attributed with hesitation to *Eusthenodon* (Young 1993), and a few possible tristichopterid fragments from Antarctic (Young *et al.* 1992).

The Canowindra fauna significantly alters this picture. *Mandageria* and the second tristichopterid account for 50% of the recorded sarcopterygian diversity at the site—(the other two genera are the canowindrid *Canowindra*, a member of the exclusively Gondwanan group, the Canowindridae, and an undescribed form of bizarre morphology and uncertain affinities (Johanson & Ahlberg, in prep.). Furthermore, *Mandageria* yields the most complete anatomical information of any tristichopterid so far described, other than *Eusthenopteron*. It thus makes a major contribution to our understanding of the Tristichopteridae.

Recently, probable tristichopterids have been discovered in Late Devonian deposits at Eden, NSW (Z.J. & P.E.A., pers. obs.) and Grahamstown, South Africa (Gess & Hiller, 1995). It thus appears that tristichopterids attained a wide distribution



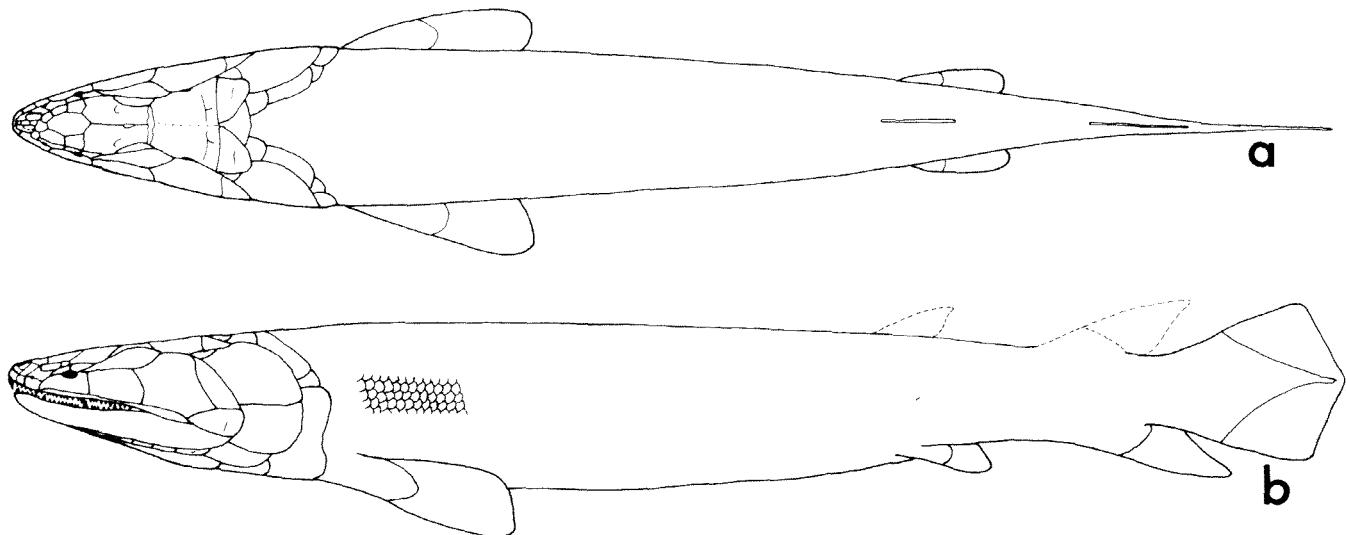
**Figure 21** *Mandageria fairfaxi*. Reconstruction of skull and shoulder girdle: (a) dorsal view; (b) lateral view. In (b), the dotted vertical line in the snout represents a break that can be interpreted either as a suture, or as a crack following the course of the supraorbital sensory canal (see Figure 14).

in Gondwana during the Late Devonian. In this context, it would obviously be interesting to know whether Gondwana tristichopterids are immediately related to each other or whether they belong on different parts of the tristichopterid tree. Unfortunately, that question cannot be answered at this stage. The Tristichopteridae have never been subjected to an overall cladistic analysis, and many of the taxa are as yet inadequately understood (we are pleased to note that the South African material is being studied by J.A. Long and South African colleagues, while O.A. Lebedev is describing superb acid-prepared material from the Andreyevka-2 locality near Tula, Central Russia). For the present, we confine ourselves to observing that *Mandageria fairfaxi* shares a number of presumably derived characters with *Eusthenodon* and can plausibly be interpreted as the sister group to that genus. Once the second tristichopterid from Canowindra has been described (Ahlberg & Johanson, in review), an attempt will be made to produce an overall phylogeny of the

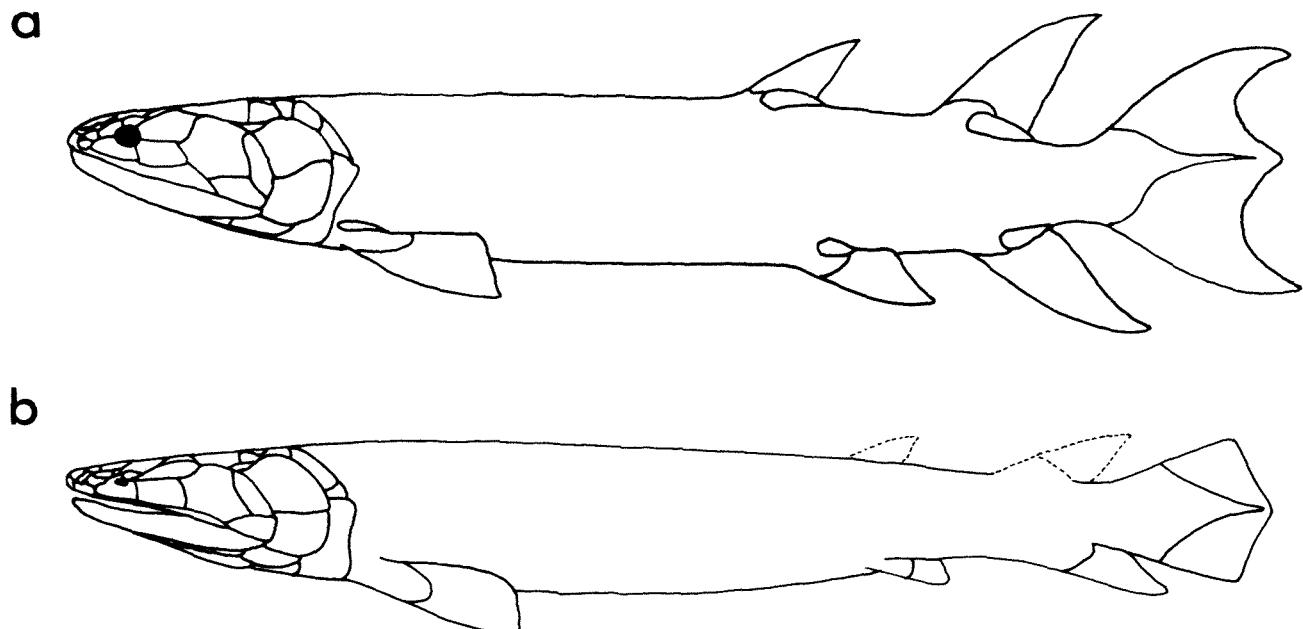
Tristichopteridae. This should help to clarify the biogeographic significance of their distribution, as well as contributing to the gradually emerging picture of osteolepiform relationships.

### Acknowledgements

Our foremost thanks go to Dr Alex Ritchie (Australian Museum, Sydney), without whose tenacity, vision and organising genius *Mandageria* would still be buried under the road from Canowindra to Gooloogong. The rediscovery and excavation of the Canowindra fish fauna was made possible by the provision of heavy earthmoving equipment by Cabonne Shire Council and extensive voluntary assistance from the Canowindra community. Zerina Johanson would like to thank Mr James Fairfax for the generous financial support of her research programme, as well as The Australian Museum for financial support and work space, the Linnean Society of NSW, the School of Earth Sciences Macquarie University,



**Figure 22** *Mandageria fairfaxi*. Body reconstruction. The proportions are taken from the holotype, F96508. (a) Dorsal view. (b) Lateral view. The total body length is approximately 160 cm.



**Figure 23** Comparison of the body morphology of (a) *Eusthenopteron* and (b) *Mandageria*, both in lateral view. Not to scale.

and Ampolex Australia for additional financial support. Per Ahlberg wishes to thank Dr Alex Ritchie for his kind invitation to join the Canowindra project, and the Natural History Museum and Dr Robin Cocks for the generous travel funding which allowed him to visit Australia and carry out this study. We also thank the referees, and Mr Oleg Lebedev, for their helpful comments which did much to improve the quality of the manuscript. Finally we wish to thank Oleg Lebedev for generously sharing unpublished information about the Andreyevka-2 *Eusthenodon* material with us.

## 5. Explanation of figure lettering

acc. vo	accessory vomer	bas.art	basal articulation
an.fin	anal fin	Cbr1–4	ceratobranchial 1–4
an.fin.b.p.	anal fin basal plate	Cho	choana
an.fin.rad	anal fin radials	Chy	ceratohyal
An	anocleithrum	Cla	clavicle
Bb1, 2	basibranchial 1, 2	Cl	cleithrum
		ca.fin(ep.)	caudal fin–epichordal lobe
		ca.fin(hyp.)	caudal fin–hypochordal lobe
		ca.fin.rad	caudal fin radial
		cap.hu	caput humeri
		De	dentary
		Dpl	dermopalatine
		delt	deltoid process
		Ect	ectopterygoid
		Ent	entoptygoid
		ect	ectepicondyle
		ent	entepicondyle
		ent.for	entepicondylar foramen
		f.ap	fossa apicalis
		f.De	dentary fang

f.Dpl	dermopalatine fang
f.Ect	ectopterygoid fang
Gu	gular
Hu	humerus
Hybr1–4	hypobranchial 1–4
Hyp	hypohyal
haem.sp	haemal spine
Id	infradentary
Int	intermedium
It	intertemporal
inter	intercentrum
Ju	jugal
La	lacrimal
Lat.Ro	lateral rostral
L.ex	lateral extrascapular
L.jaw	lower jaw
M.ex	median extrascapular
M.gu	median gular
Mx	maxilla
M.po.ro	median postrostral
mesIV	mesomere 4
Na	nasal bone
nar	narial opening
neur.sp	neural spine
n. spir	spiracular notch
Op	opercular
oa.P.So.	overlap area for posterior supraorbital
orb	orbit
Pa	parietal
Pp	postparietal
Pmx	premaxilla
Po	postorbital
Pop	preopercular
Pos	postspiracular
Pot	posttemporal
Pr.Pmx	posterior process of premaxilla
Psp	parasphenoid
pi	pineal foramen
pit	pit on surface of humerus
pitl.	pitline
proc.hu	humeral process
Ra	radius
Ro	rostral
radIII	third radial
Scap	scapulocoracoid
So	supraorbital
So.ol	overlap area of supraorbital
Sop	subopercular
Sq	squamosal
Su	supratemporal
Sub.br	submandibulo–branchiostegal
sub	submandibular
sub.ol	overlap area of submandibular
Suc	supracleithrum
subl	sublingual rod
Ta	tabular
Te	tectal
t.Pmx	enlarged premaxillary tooth
f.Vo	vomerine fang
Ul	ulna
Ulr	ulnare
Uro	urohyal
Vo	vomer

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Z. JOHANSON, Palaeontology Section, Australian Museum, 6 College Street, Sydney, NSW, 2000, Australia,  
and MUCEP, School of Earth Sciences, Macquarie University, NSW, 2109, Australia.  
P. E. AHLBERG, Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK.

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