

EOCENE SPIDERS FROM THE ISLE OF WIGHT WITH PRESERVED RESPIRATORY STRUCTURES

by PAUL A. SELDEN

ABSTRACT. A new fossil spider, *Vectaraneus yulei* gen. et sp. nov., from the Eocene Bembridge Marls Insect Bed of the Isle of Wight, shows internal anatomy, including book lungs and tracheae, preserved by calcium carbonate replacement. The wide, medially positioned, tracheal spiracle and large tracheae which enter the prosoma are adaptations for an amphibious mode of life. The spider is placed in Cybaeidae Simon, 1898, Argyronetinae Menge, 1869, a subfamily which includes the Recent European Water Spider, *Argyroneta aquatica* (Clerck, 1757). The only previously described Bembridge Marls spider, *Eoatypus woodwardii* McCook, 1888, is redescribed; it is unrelated to *Vectaraneus*. The holotype of *Argyroneta antiqua* Von Heyden (1859) is redescribed; it is not an *Argyroneta*. Specimens referred to *A. antiqua* by Bertkau (1878) probably belong in Argyronetinae Menge, 1869, and this subfamily is emended herein.

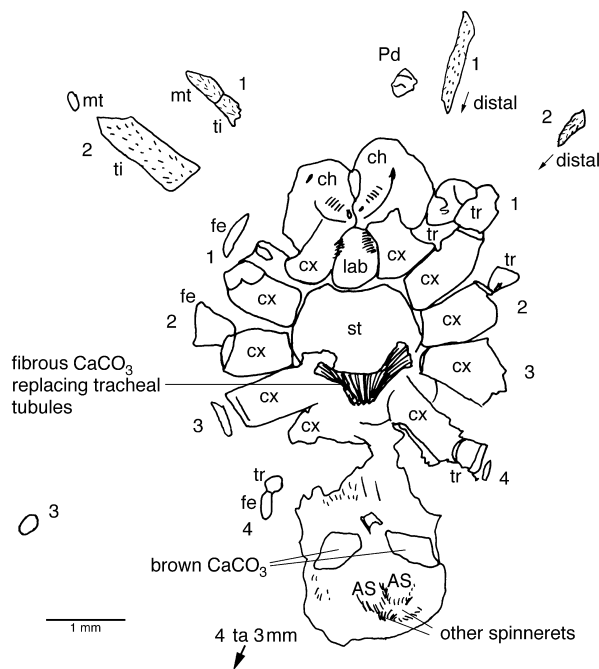
KEY WORDS: Araneae, *Argyroneta*, Arthropoda, Cybaeidae, tracheal system.

SPIDERS are rare as fossils in sedimentary rocks, excluding amber, so that when they do occur the preservation is generally remarkable and the horizon may be classified as a fossil Konservat-Lagerstätte (Selden 1989). Insects from the Eocene Bembridge Marls of the Isle of Wight are well known for showing excellent preservation of internal anatomy in calcite (McCobb *et al.* 1998). In the present paper, specimens of a new spider, *Vectaraneus yulei* gen. et sp. nov., are described, which show the same remarkable preservation of internal structures, including musculature, book lungs, and the tracheal system. The tracheae consist of an unusually large pair of median trunks, arising from a wide spiracle situated medially on the ventral opisthosoma, and extending forwards as finer tubes into the prosoma. Such an arrangement is typical of active and amphibious spiders. A review of the morphology of *Vectaraneus* suggests it belongs in Cybaeidae Simon, 1898, Argyronetinae Menge, 1869, a subfamily which includes the European Water Spider, *Argyroneta aquatica* (Clerck, 1757). An amphibious mode of life accords with sedimentological and palaeoecological evidence from the Bembridge Marls, which indicates a palaeoenvironment of a shallow, alkaline, freshwater lake (McCobb *et al.* 1998).

Specimen BMBN 021960/1 was brought to my attention by the collector, Dr E. A. Jarzembowski (Maidstone Museum). A survey of collections containing other Bembridge Marls spiders, in the Museum of Isle of Wight Geology, Sandown, and The Natural History Museum, London, revealed a few conspecifics, descriptions of which are included here. Spiders are discovered occasionally in the Bembridge Marls Insect Bed (e.g. Jackson 1938; Jarzembowski 1976) but rarely are described. The holotype and only known specimen of the only previously described Isle of Wight Tertiary spider, *Eoatypus woodwardii* McCook, 1888, is redescribed in this study, as is the holotype of *Argyroneta antiqua* Von Heyden (1859), from the Miocene Brown Coal of Germany. The collection of Bembridge Marls spiders in The Natural History Museum, London, consists of about 50 specimens, belonging to a number of species, so that there is more work yet to be done describing these, and biodiversity studies could also prove interesting.

STRATIGRAPHY AND PRESERVATION

Specimen BMBN 021960/1 comes from the so-called Insect Bed of the upper Eocene Bembridge Marls Member of the Bouldnor Formation (Solent Group) of Thorness Bay, Isle of Wight (stratigraphy follows



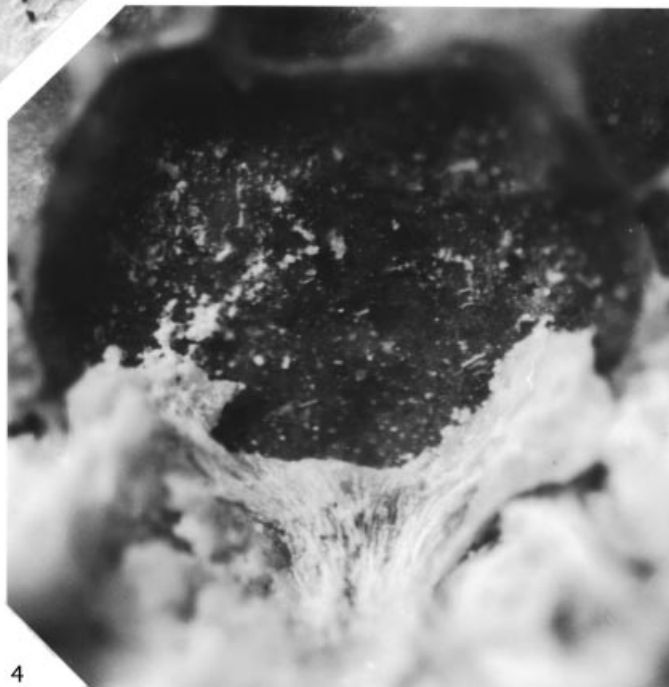
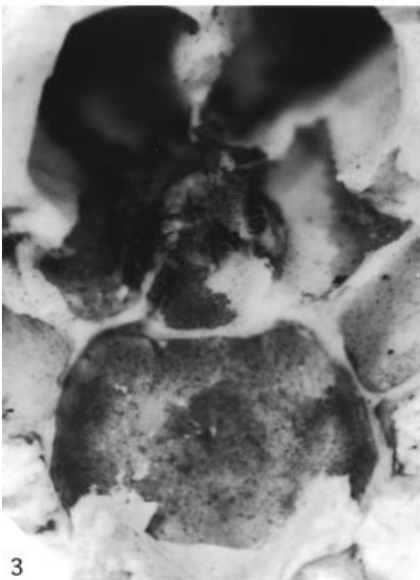
TEXT-FIG. 1. *Vectaraneus yulei* gen. et sp. nov., upper Eocene, Bembridge Marls, Isle of Wight. Camera lucida drawing of paratype, BMNH In 17151. See text for abbreviations.

Insole *et al.* 1998). IWCMS 1999.6 is also from Thorness Bay; all other specimens and *Eoatypus* are from Gurnet (= Gurnard) Bay. The matrix is a massive, fine limestone which resembles the lithology of the main, tabular, insect-bearing horizon which occurs near the base of the Bembridge Marls (see Jarzembowski 1980 and McCobb *et al.* 1998, for more details). In the same block as BMBN 021960/1 are some arthropod fragments (identified as the crustacean *Branchipodites vectensis* on the museum label) and pieces of the reed *Typha*. Other specimens bear insects and other biota; cursory examination reveals the presence of *Typha*, Hymenoptera, Diptera, and juvenile Araneae, commonly in distinct horizons (suggesting mass mortality, e.g. following a synchronous emergence) or aggregations (suggesting accumulation by water surface tension or adhesion to floating vegetation). BMNH I 8438 has a number of small, stellate bodies which may be leaf hairs. The palaeoenvironment of deposition suggested by the sedimentology is a shallow, freshwater, alkaline lake (McCobb *et al.* 1998). Associated plants, insects, and mammals suggest an open marsh habitat with wooded islands in a subtropical climate (Jarzembowski 1980; Collinson 1983, 1990; Collinson *et al.* 1993).

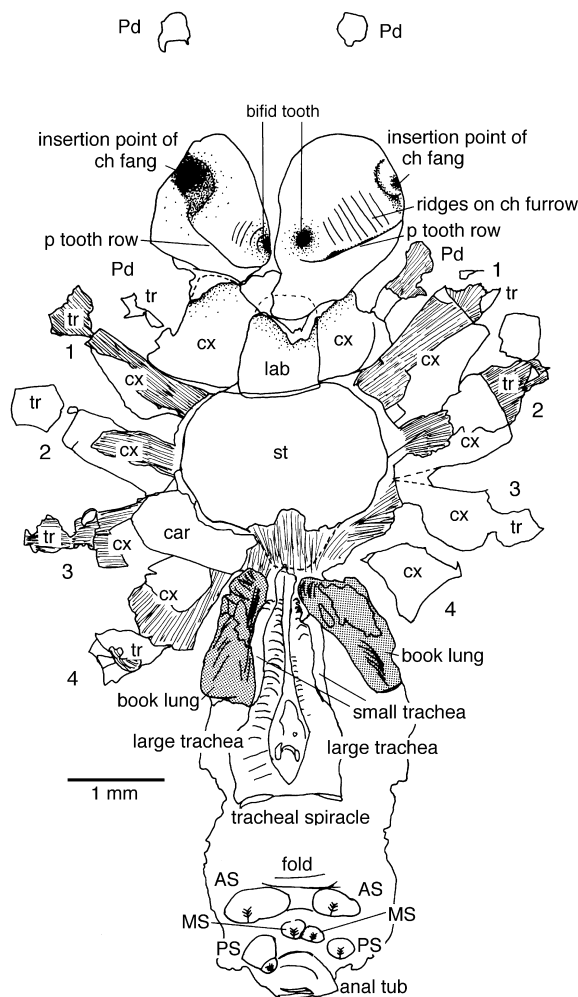
The most remarkable aspect of the Bembridge spiders is the extremely fine preservation of internal anatomical structure. Some organic matter is preserved, mainly thin laths of cuticle lining the external

EXPLANATION OF PLATE I

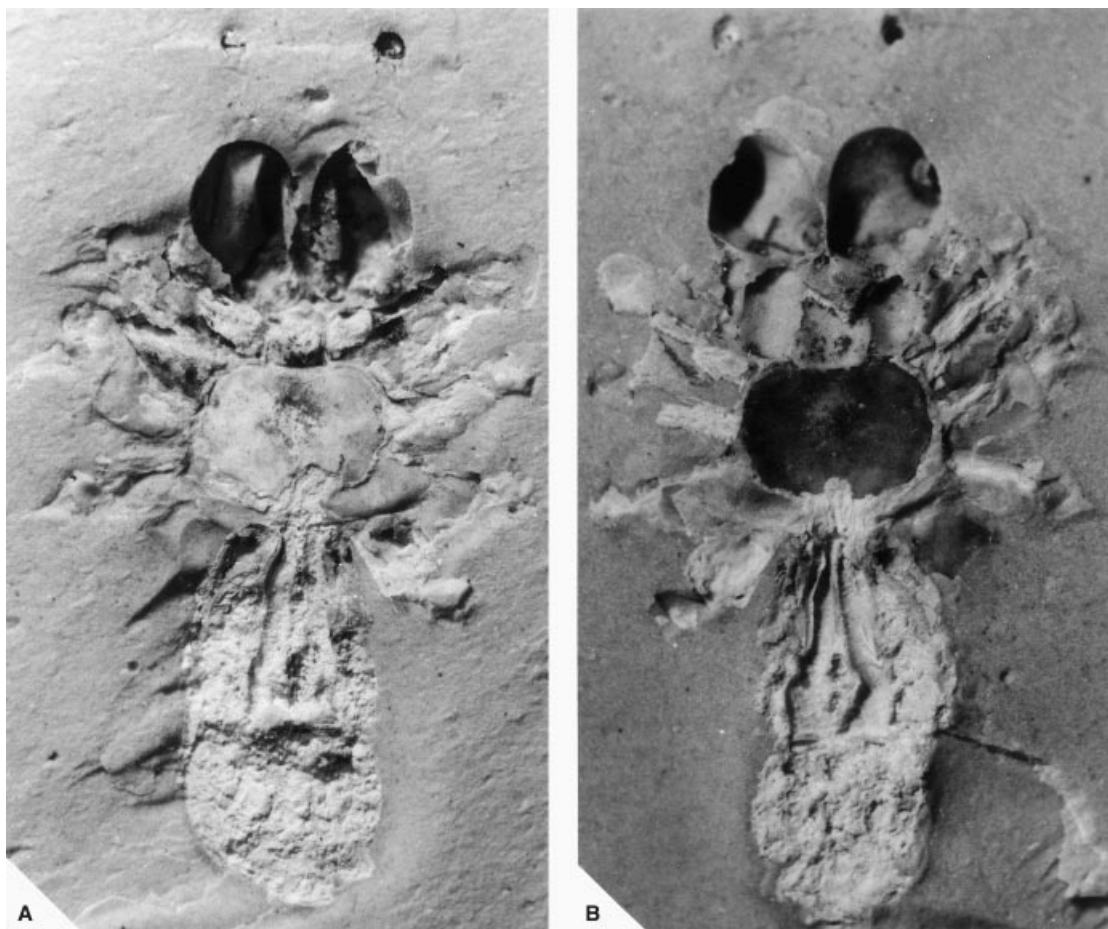
Figs 1–4. *Vectaraneus yulei* gen. et sp. nov., upper Eocene, Bembridge Marls, Isle of Wight. 1, holotype part, BMBN 021960; ventral side of animal; see Text-figure 2 for explanation; $\times 11$. 2–4, paratype, BMNH In 17151. 2, ventral side of animal showing opisthosoma with spheroidal calcite infill before its removal to reveal spinneret moulds; see Text-figure 1 for explanation; $\times 16$. 3, detail of sternum, labium, pedipalp coxae and chelicerae; $\times 27$. 4, detail of sternum showing fibrous calcite replacement of fine tracheal tubes on entering prosoma from pedicel; $\times 48$.



mould cavities of the chelicerae, and setae within the rock which can be seen when the specimens are observed under alcohol. Within the moulds of the chelicerae, labium, and coxae, fine fibres of cream-coloured calcite can be seen. Presumably, these represent muscle fibres replaced by calcite during diagenesis, as described for the Bembridge Marls insects by McCobb *et al.* (1998). In the opisthosoma, book-lung lamellae are preserved in buff-coloured calcite, and the book-lung atria anterior to the lamellae are lined with tiny, buff, drusy calcite crystals. Much of the opisthosoma of BMBN 021960/1 is filled with cream-coloured calcite, which strikingly preserves the large tracheae as tubes running forward from the wide spiracle near the middle of the opisthosoma. The inner surfaces of these tubes bear reinforcements preserved in the same cream calcite. The posterior part of the opisthosomas of BMBN 021960/1 and In 17151 (Pl. 1, figs 1–2; Text-figs 1–5) were filled with calcite which shows a spheroidal structure in places. This could represent silk glands or ova, or could be botryoidal mineral growth inside a cavity. The common preservation of Bembridge Marls insects as cuticle-lined external moulds, without internal



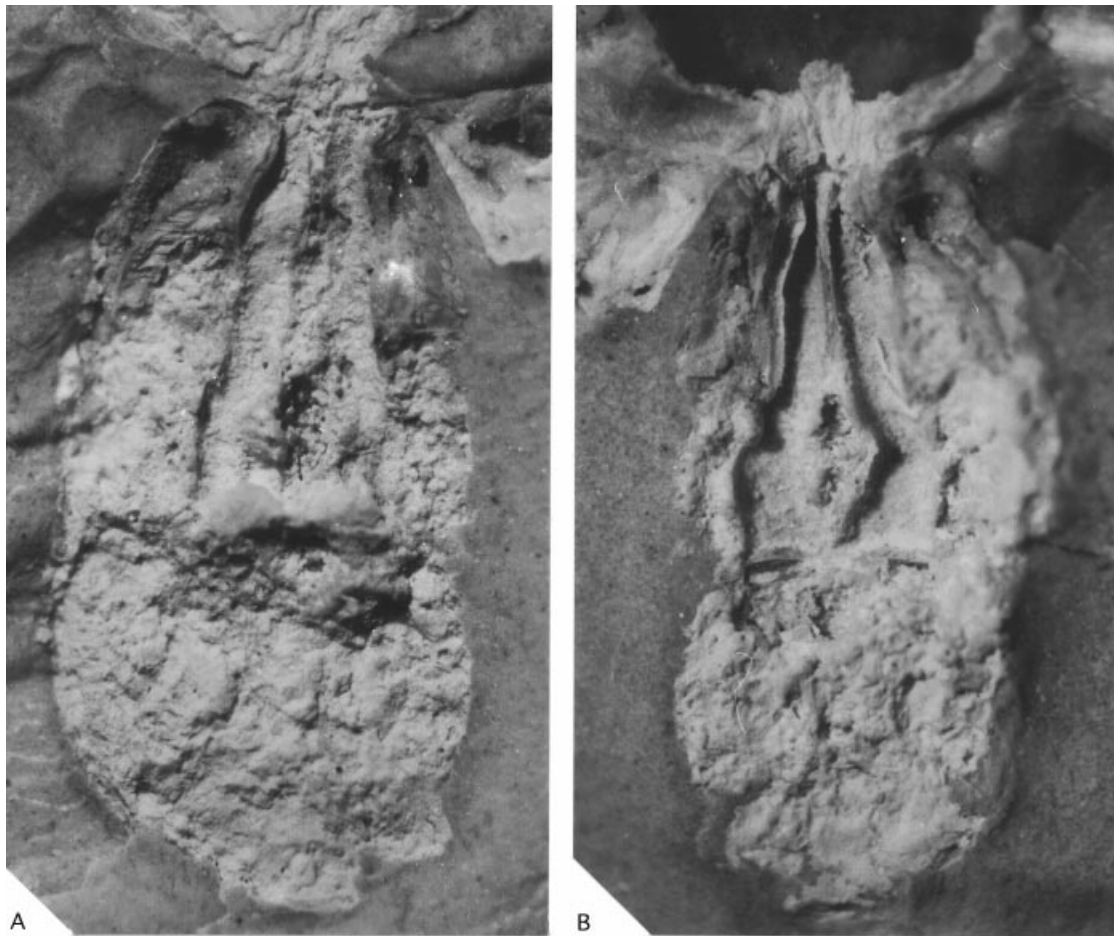
TEXT-FIG. 2. *Vectaraneus yulei* gen. et sp. nov., upper Eocene, Bembridge Marls, Isle of Wight. Camera lucida drawing of holotype part, BMBN 021960. Dashed line shows rear edge of sternum after excavation of fibrous calcite replacing fine tracheae. Spinnerets shown after removal of calcite spheroids. See text for abbreviations.



TEXT-FIG. 3. A–B, *Vectaraneus yulei* gen. et sp. nov., upper Eocene, Bembridge Marls, Isle of Wight; holotype part and counterpart, dry; $\times 12$. A, counterpart, BMBN 021961, showing dorsal external mould of chelicerae, internal mould of sternum, labium, pedipalp coxae, spiracle and tracheal sacs. B, part, BMBN 021960, before removal of calcite from opisthosoma and posterior sternum; ventral external mould of chelicerae, pedipalp coxae, labium and sternum; note wide spiracle leading to large tracheae with spiral or annular thickenings. See Text-figure 2 for explanation.

mineralization, was mentioned by McCobb *et al.* (1998), so the later full or partial infilling of the voids by calcite is likely. This spheroidal calcite was removed to reveal the spinnerets. Because of the preservation of internal anatomy, and their three-dimensional nature, most of the fossils must represent dead animals rather than moults.

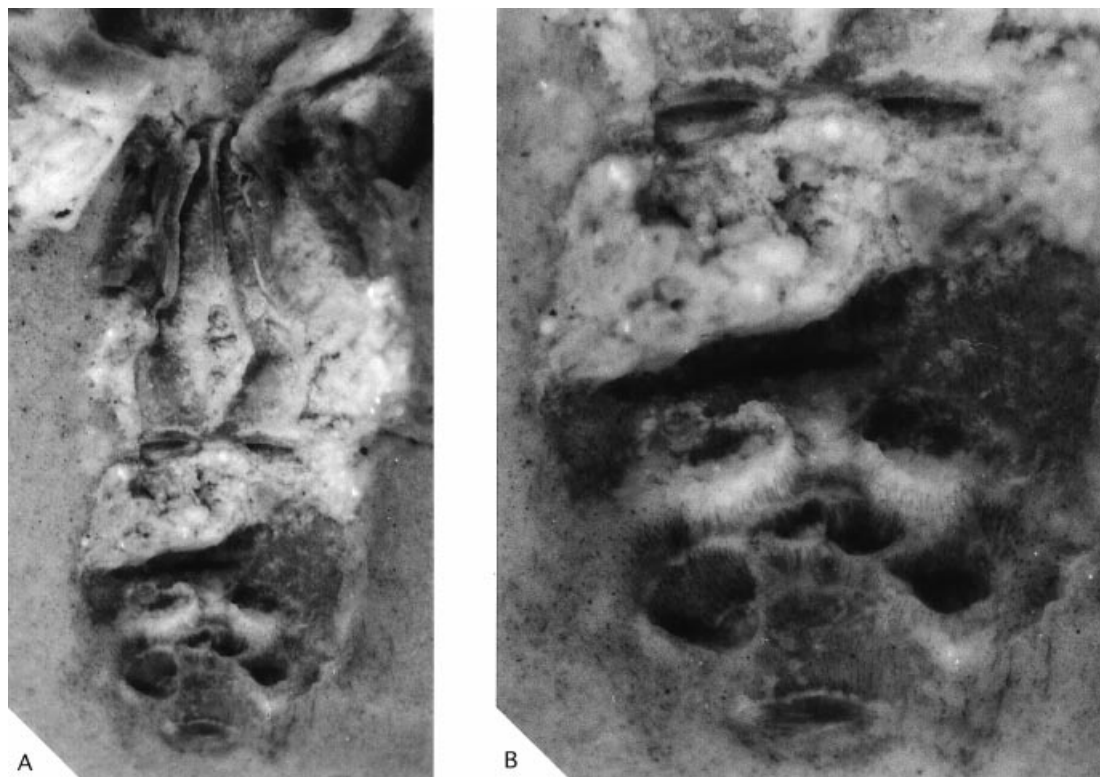
Specimens of *Vectaraneus* were recognized by their preservation of tracheae in the same manner as in BMBN 021960/1. Why should tracheae, of all internal anatomy, be preferentially preserved? Tracheae are resistant structures, as evidenced by Platnick's (1974, p. 210) description of his method for revealing tracheal systems in anyphaenids: 'Tracheae were examined by dissecting away the dorsal cuticle of the abdomen and boiling the spider in ten percent sodium hydroxide for ten minutes. By this method, all the soft structures in the abdomen are digested away, leaving the tracheae intact'. Median tracheae are derived from apodemes (see below), and are therefore ectodermal; functionally, tracheae are non-porous, open-ended tubes, which need to be strong to prevent collapse during movements of the rest of the body. Thus,



TEXT-FIG. 4. A–B. *Vectaraneus yulei* gen. et sp. nov., upper Eocene, Bembridge Marls, Isle of Wight; holotype part and counterpart, opisthosoma, dry; $\times 23$. A, counterpart, BMBN 021961, showing book-lung lamellae preserved in darker calcite and infill of tracheal sacs. B, part, BMBN 021960, before removal of calcite, showing wide spiracle and large tracheae with spiral or annular thickenings, dividing into two tracheae before splitting into finer tubes at pedicel. See Text-figure 2 for explanation.

not only are they relatively preservable, their morphology is distinct, unlike silk glands, for example, which are rather amorphous.

The part of BMBN 021960 is preserved as a ventral mould with replacement of some internal structures, as detailed above; the counterpart (BMBN 021961) is a dorsal external mould but showing mostly internal structures of the ventral, such as the sternum. All specimens are preserved in the same way as BMBN 021960/1, though are generally less complete. IWCMS 1999.6 is a ventral mould with little internal replacement. Scattered on the surface of this block, and in parts of the specimen, is a soft, white deposit which does not react to 10 per cent HCl, and resembles kaolinite. BMNH In 17151 is a ventral mould with considerable internal replacement of coxae of legs 2–4, the posterior part of the sternum, and the opisthosoma. Distal podomeres of some anterior legs are preserved on this specimen. BMNH I 8438 shows least detail of all specimens, but careful preparation has revealed more information, confirming that the specimen belongs to the species described here. The specimen is a ventral external mould with the right

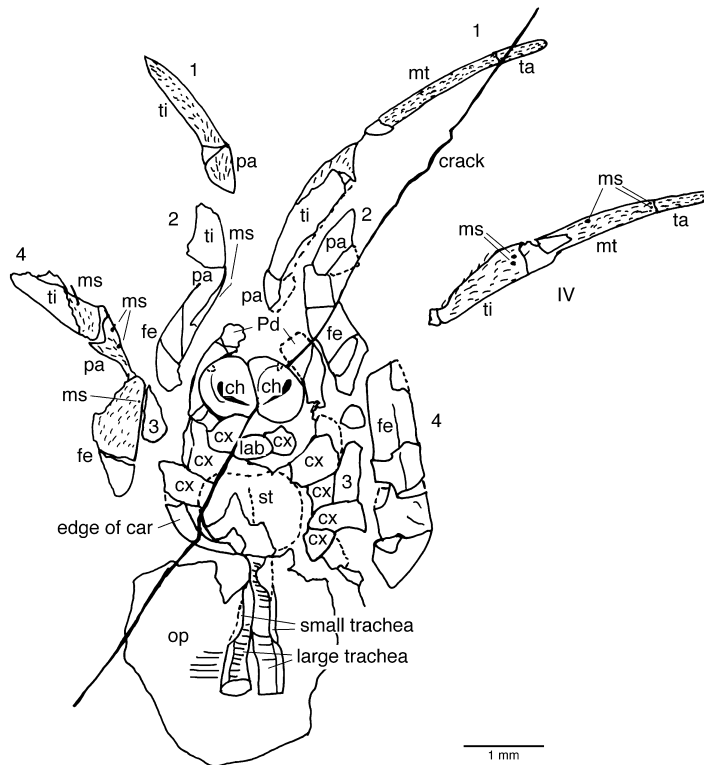


TEXT-FIG. 5. A-B. *Vectaraneus yulei* gen. et sp. nov., upper Eocene, Bembridge Marls, Isle of Wight; holotype part, BMBN 021960, under ethanol. A, opisthosoma with spheroidal calcite removed, showing book-lung lamellae (left and right anterolateral), wide spiracle and large tracheae with spiral or annular thickenings, and spinnerets and anal tubercle in posterior part; preserved in darker calcite and infill of tracheal sacs; $\times 20$. B, detail of posterior half of opisthosoma, showing wide tracheal spiracle, and external moulds of spinnerets and anal tubercle; $\times 40$. See Text-figure 2 for explanation.

chelicera crushed across the anterior labium and left pedipalp coxa. The posterior opisthosoma and spinnerets are missing because the rock is broken away. Many other fossils occur on this small piece of rock, including a spiderling (though not necessarily of this species). BMNH I 8440 and I 8452 (part and counterpart, respectively) are ventral and dorsal moulds, respectively. I 8440 has a repaired fracture running obliquely across the middle of the specimen (Pl. 2; Text-fig. 6). The opisthosoma is not calcite-filled but flattened; the remainder of the specimen, however, is three-dimensionally preserved. Careful preparation has revealed fine details of the distal podomeres of legs 3 and 4.

Eoatypus woodwardii is preserved on the surface of a piece of limestone which was weathered before collection. The surface bearing the spider is smooth. The fossil is an external mould of the dorsal surface, with some remaining adherent soft white material in places (which is easily removed). This material could be the same ?kaolinite reported above on IWCMS 1999.6. At the lateral borders of the carapace, impressions of the distal parts of the coxae and the trochanters hide the edge of the carapace. Under alcohol there is no trace of cuticle or setae, making identification of the podomeres and other parts of the spider unusually difficult.

Argyroneta antiqua Von Heyden (1859) comes from the Kiesel-schiefer facies of the Miocene Brown Coal at Stöschen pit near Linz am Rhein, Germany. It is preserved as dark brown coloration on a lighter brown paper shale. Adjacent to the specimen is a plant stem. Leg podomeres are discernible (cf.



TEXT-FIG. 6. *Vectaraneus yulei* gen. et sp. nov., upper Eocene, Bembridge Marls, Isle of Wight. Composite camera lucida drawing of paratype, BMNH I 8440 (part), and BMNH I 8452 (counterpart). See text for abbreviations.

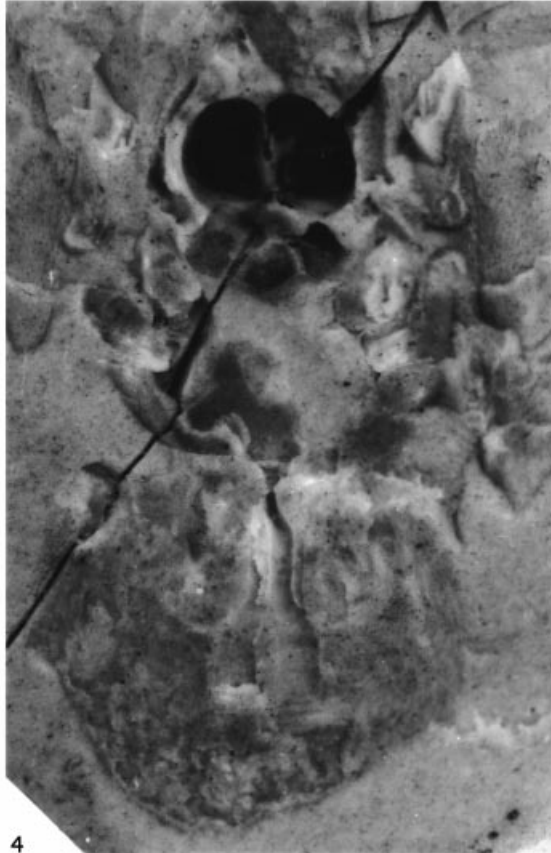
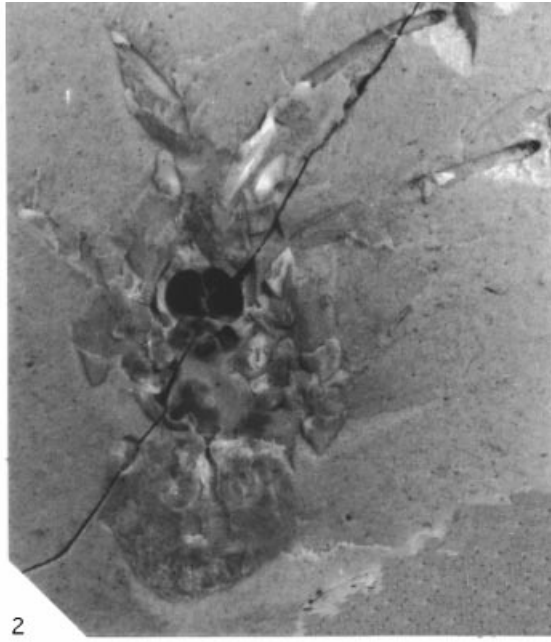
Petrunkévitch 1946 who claimed they were not), as are the outlines of the chelicerae, palpal cymbiums, and abdomen, though no structural details can be seen.

METHODS

An attempt was made to view the counterpart of BMBN 021960/1 using scanning electron microscopy of the uncoated specimen in an environmental chamber, but this revealed no more information than could be seen with light microscopy. The specimens were studied under a Wild M7S stereomicroscope, drawn with a camera lucida attachment, and photographed using Minolta and Praktica cameras on the Wild. They were studied both dry and under alcohol; the latter showed up any organic cuticular matter and setae well. In the Bembridge Marls specimens, it was necessary to remove the calcite from a few places, in order to reveal hidden morphology (e.g. the posterior border of the sternum, and the spinnerets in BMBN 021960/1; the left chelicera, spinnerets, and abdominal setation in BMNH I 8438). For this, a hypodermic needle mounted on an aquarium air pump, as detailed in Selden and Shear (1996), was used. Using this device, gentle pressure causes the deposit to break off and is immediately blown away so that the preparation area is kept free of debris and no more matrix than necessary is removed.

EXPLANATION OF PLATE 2

Figs 1–4. *Vectaraneus yulei* gen. et sp. nov., upper Eocene, Bembridge Marls, Isle of Wight; paratype, BMNH I 8440. 1, 3 dry; 2, 4 under ethanol. 1–2 whole specimen; $\times 8.5$. 3–4 body only; $\times 19.5$. See Text-figure 6 for explanation.



Comparative material

The following is the most important Recent material which was studied for comparative purposes; all is in the author's collection, unless otherwise stated. Anyphaenidae: *Amaurobioides maritimus* O. P.-Cambridge, 1883, ♀, Dunedin, New Zealand (coll. CAS); *Anyphaena accentuata* (Walckenaer, 1802), ♀, 10.VI.96, Carnac, France (coll. D. Penney); *Hibana similis* (Banks, 1929), ♀, 3.XII.95, El Valle, Panama (coll. D. Penney); Cybaeidae: *Argyroneta aquatica* Clerck, 1757, ♀, 18.VI.81, Whixall Moss, Shropshire, England; ♂, commercial slide, compressed mount (dated 1895); *Cybaeus hesper* Chamberlin and Ivie, 1932, ♂, 30.X.98, Redwood grove, Monte Rio, Sonoma Co., California; *Cybaeus patritus* Bishop and Crosby, 1926, ♀, 15.VII.96, Highlands Biological Station, Macon Co., North Carolina.

Terminology and abbreviations

All measurements are in millimetres (mm). Standard leg formulae are used; e.g. 1423 indicates that walking leg 1 is the longest, 4 the next longest, and 3 the shortest. Abbreviations: 1, 2, 3, 4, walking legs 1–4; AS, anterior spinneret; car, carapace; ch, chelicera; cx, coxa; lab, labium; MS, median spinneret; ms, macroseta; op, opisthosoma; p, posterior; Pd, pedipalp; pm, promargin(al); PS, posterior spinneret; rm, retromargin(al); st, sternum; tr, trochanter; tub, tubercle. Repository codens: BMBN, Booth Museum of Natural History, Brighton; BMNH, The Natural History Museum [British Museum (Natural History)], London; CAS, California Academy of Sciences, San Francisco; IWCMS, Museum of Isle of Wight Geology, Sandown; LACM, Los Angeles County Museum of Natural History; MMUE, The Manchester Museum.

MORPHOLOGICAL INTERPRETATION

Vectaraneus

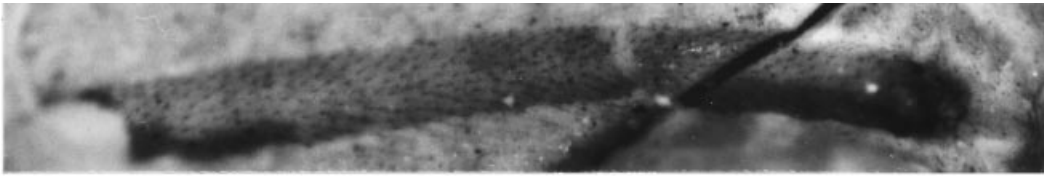
The following interpretation is based on the holotype, BMBN 021960/1, with additional information from other specimens where necessary.

Carapace. Only a small part of the posterior edge of the carapace is preserved on BMBN 021960/1, on both part and counterpart. It appears to be dorsally concave along the border. This observation is confirmed in BMNH I 8440/I 8452, which shows a similar concave postero-lateral corner (Pl. 2, figs 3–4; Text-fig. 6). BMNH I 8452 (Pl. 3, figs 4–5) shows the dorsal external mould of the anterior carapace preserved in the roof of the cheliceral mould space. Taking into account the dimensions of the preserved parts of the posterior border of the carapace, and the anterior outline of the chelicerae, the carapace would have been broadly pyriform in life, with generally parallel lateral edges in the post-cephalic part, and somewhat narrower anteriorly.

Chelicera. The chelicerae are preserved as external moulds with some adherent cuticle on the surfaces. They appear large, but chelicerae generally appear large in fossil spiders because the rock splits through them at the thickest point, revealing their true size; in life, they are somewhat hidden by the carapace; however, the chelicerae in the fossil appear not to be geniculate. The area where the anterior and lateral faces meet is rather angular in IWCMS 1999.6 and BMNH In 17151. On BMBN 021960 (ventral), a large

EXPLANATION OF PLATE 3

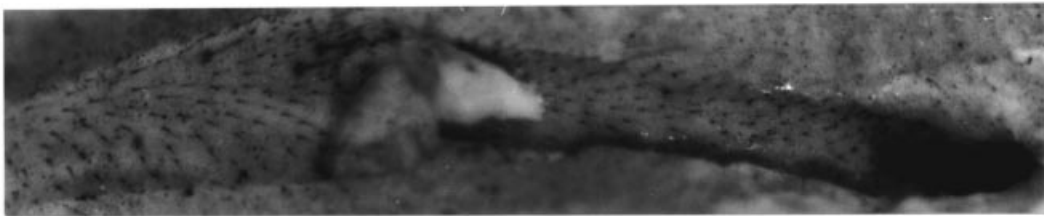
Figs 1–5. *Vectaraneus yulei* gen. et sp. nov., upper Eocene, Bembridge Marls, Isle of Wight. 1–3, paratype part, BMNH I 8440, under ethanol. 4–5, paratype counterpart, BMNH I 8452, dry. 1, leg 1 mt and ta; ×50. 2, leg 1 ta; ×200. 3, leg 2 distal ti, mt, and proximal ta; note macrosetae; ×36. 4, whole specimen, showing external mould of ventral chelicerae, internal mould of labium, pedipalp coxae, and sternum; ×10. 5, body only, same details as 4, and tracheae in abdomen; ×20. See Text-figure 6 for explanation.



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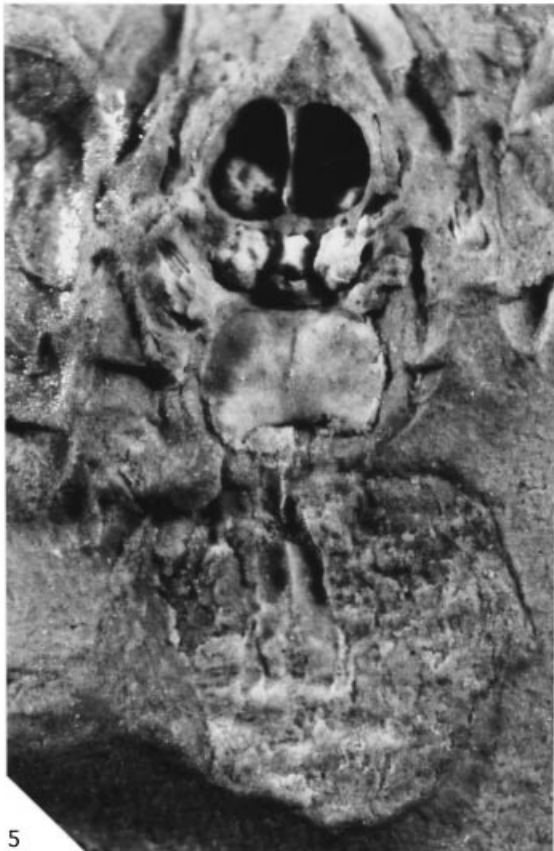
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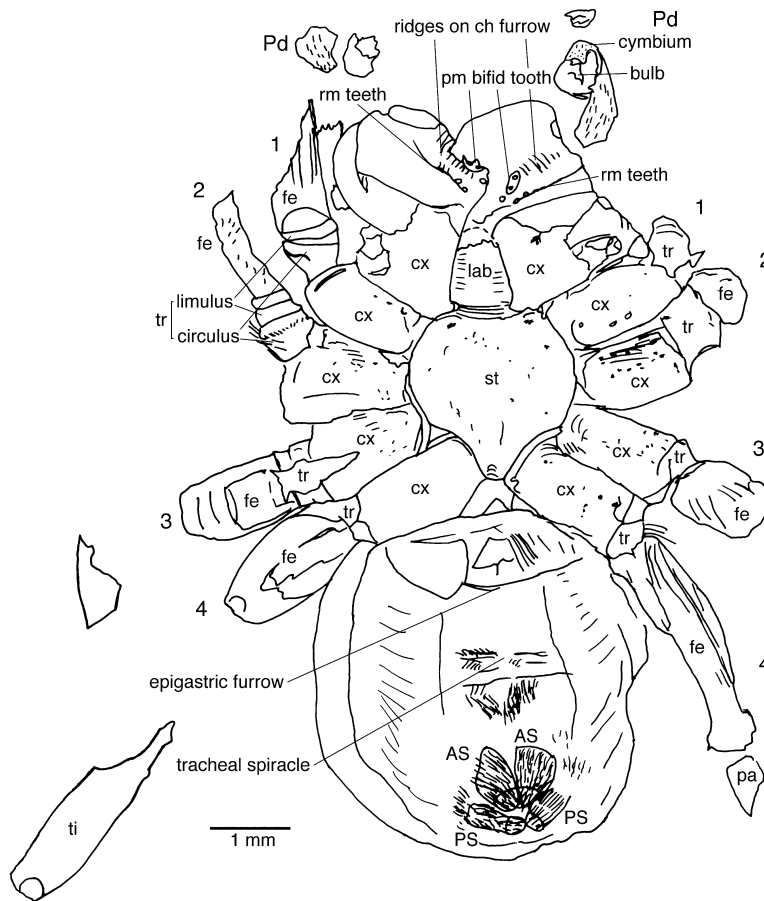
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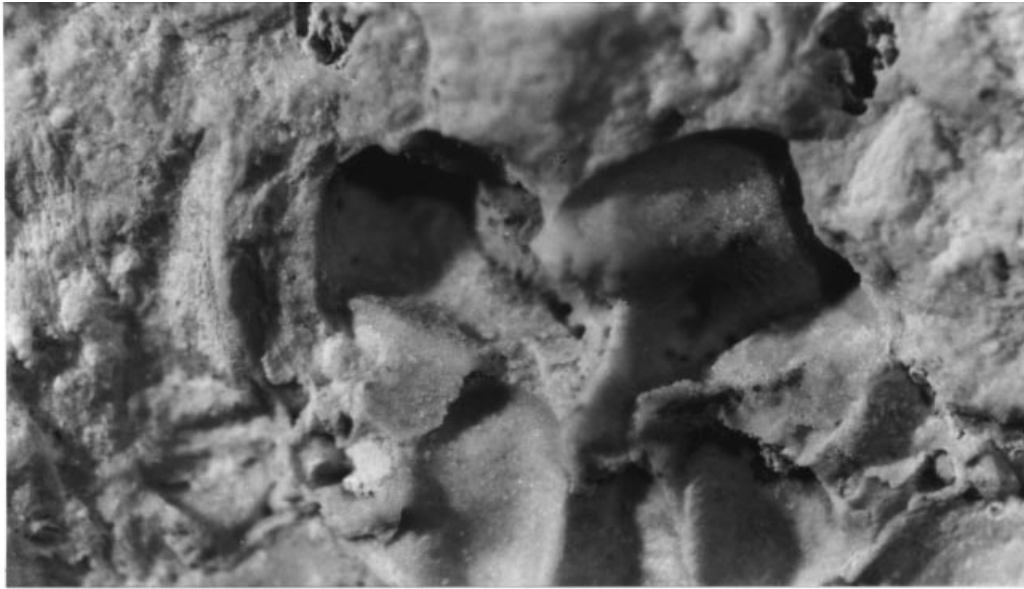


TEXT-FIG. 7. *Vectaraneus yulei* gen. et sp. nov., upper Eocene, Bembridge Marls, Isle of Wight. Camera lucida drawing of paratype, IWCMS 1999.6. See text for abbreviations.

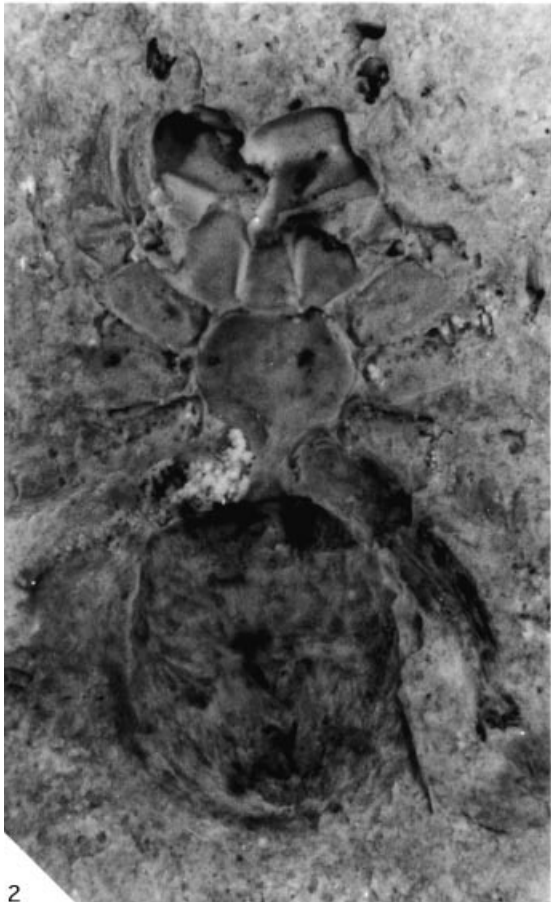
hole distolaterally on the inferior surface of the chelicera body marks the base of the fang; another conical and deep hole proximally on the inferior surface of the chelicera body, nearly the same size as the fang mould, marks a prominent tooth. On IWCMS 1999.6 (Pl. 4, fig. 1; Text-fig. 7) and BMNH I 8438 (Text-figs 8–9), this hole can be seen to represent two contiguous teeth in life, or rather a single bifid (fissidentate) tooth. There is another tooth proximal to the bifid tooth, adjacent to the presumed position of the fang tip. On BMBN 021960, running between the fang base and the large tooth, is a narrow groove, curving laterally, which marks the retromargin of the cheliceral furrow. The groove deepens away from the fang base, terminating in a fairly discrete hole. On other specimens, and especially IWCMS 1999.6, this

EXPLANATION OF PLATE 4

Figs 1–3. *Vectaraneus yulei* gen. et sp. nov., upper Eocene, Bembridge Marls, Isle of Wight; paratype, IWCMS 1999.6. 1, 3 dry; 2, under ethanol. 1, external mould of ventral chelicerae, showing promarginal bifid tooth, retromarginal teeth, and ridges on cheliceral furrow, also anterior parts of labium and pedipalp coxae; $\times 23$. 2–3, complete specimen; $\times 10$. See Text-figure 7 for explanation.



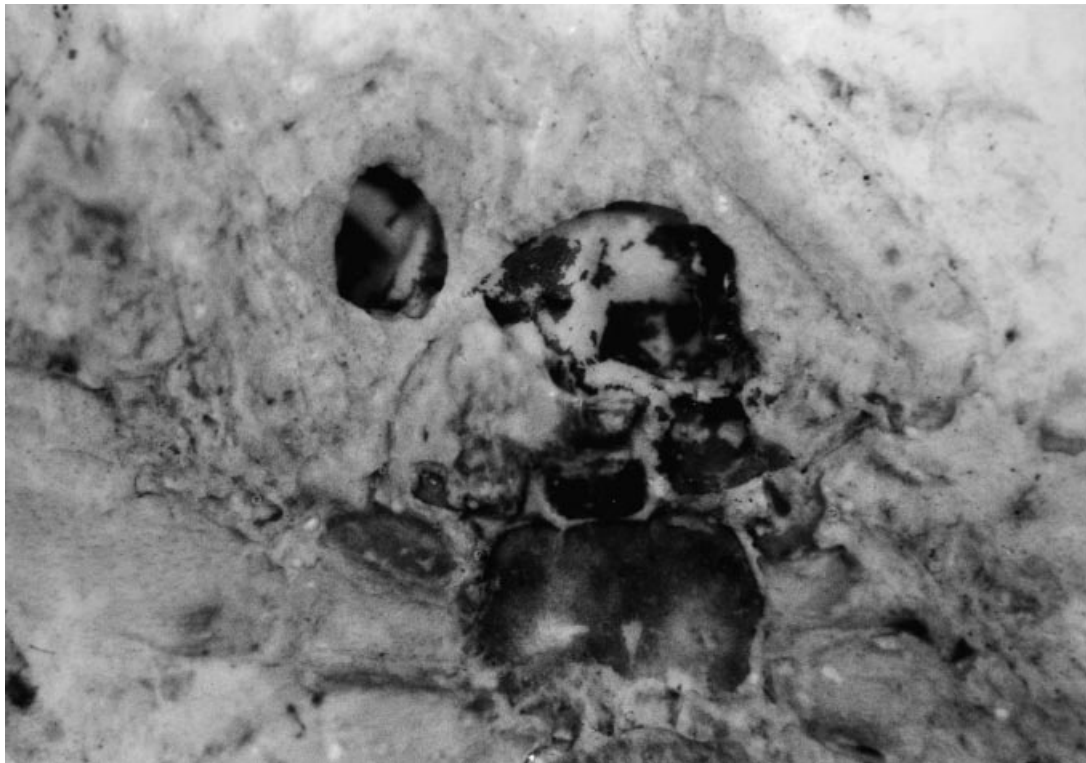
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TEXT-FIG. 8. *Vectaraneus yulei* gen. et sp. nov., upper Eocene, Bembridge Marls, Isle of Wight; paratype, BMNH I 8438, under ethanol. Anterior body showing external moulds of chelicerae, labium, pedipalp coxae, and sternum with cuticle attached; also proximal parts of anterior legs; $\times 23$. See Text-figure 9 for explanation.

groove is seen have two tooth-holes at its proximal end, which thus represent two retromarginal teeth and a carina or row of closely spaced denticles (i.e. serrate carina) in life. The fang basal hole is situated at the distalmost tip of the chelicera, and in life the fang was orientated so that its tip pointed inwards and upwards when at rest.

The cheliceral furrow is a broad col between the distal teeth and the base of the fang. It bears no promarginal teeth beyond those at the proximal end, mentioned above, but there are about seven grooves on its surface on the right chelicera of BMBN 021960 (they are present but less obvious on the left). The grooves are transverse to the length of the furrow and represent ridges in life. On IWCMS 1999.6 about ten ridges can be seen on the cheliceral groove, together with about three minor ridges on the base of the large promarginal tooth pair. Similar ridges or wrinkles occur in many spider chelicerae but rarely on the cheliceral furrow. For example, Forster (1970, fig. 107) illustrated wrinkles on the modified chelicera of the male of the desid *Helsonia plata* Forster, 1970, and *Argyroneta aquatica* has a few wrinkles close to the fang base. The position of the ridges precludes their use as a stridulatory device, such as seen, for example, on the lateral surfaces of the chelicerae of linyphiid spiders. The ridged surface may have aided gripping prey within the subchelate chelicera. The size and disposition of the fang can be inferred from the position of the fang base (e.g. seen in BMBN 021960), the likelihood that the fang tip would have rested between the proximal ends of the pro- and retromarginal teeth, and moulds of the fang seen in BMNH I 8440 and IWCMS 1999.6. The chelicera bears a prominent boss (condyle) anterolaterally on the proximal rim, as seen on specimen BMNH I 8452. Text-figure 10 is a reconstruction of the anterior view of the chelicerae.

The sternum is clearly defined. On BMBN 021960 it is convex and preserves tiny scraps of cuticle over its surface together with short, stiff setae pointing anteriorly, over the entire surface. The counterpart

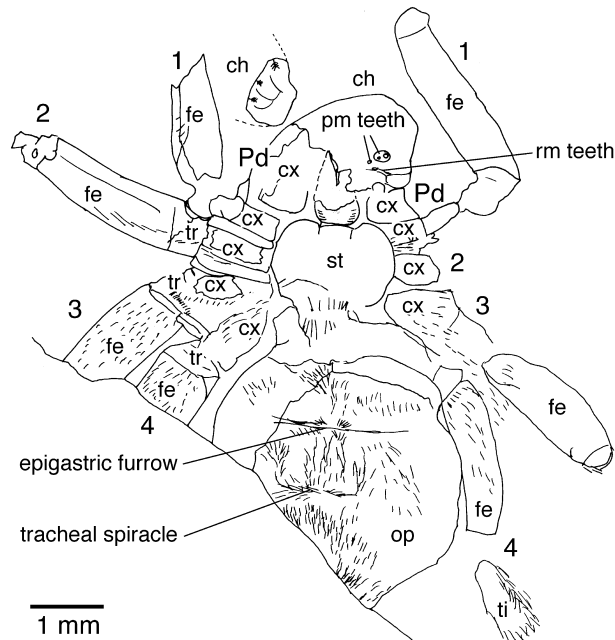
preserves the internal mould of the sternum (essentially, calcite replacement of internal tissues above the sternum). The anterior border is gently procurved, the lateral borders are gently scalloped. The posterior margin in BMBN 021960 was covered in the midline by the calcite replacement of tissues passing through the pedicel, but removal of the calcite on one side revealed that the sternum is strongly produced between the coxae of leg 4 on its posterior margin. Other specimens confirm the heart-shaped sternum produced between the coxae of leg 4. Specimen BMNH I 8438 has sternum cuticle preserved and shows, amongst the many setal follicles present across the surface, a pair of slit sensilla approximately one-quarter of the sternum length behind the anterior margin, and one-quarter of the width in from the lateral margins; the slits are angled so that they converge forwards (Pl. 5, fig. 1).

The pedipalp coxa bears a large, subquadrate endite with many setae on its mesial edge (e.g. BMNH In 17151). On specimens in which cuticle is preserved (BMNH In 17151, IWCMS 1999.6), a dark line marks the mesial edge of the coxa; on BMNH I 8440, a serrate line distolaterally on the left pedipalp coxa marks a possible serrula. The labium is elongate, with gently anteriorly converging lateral edges, not rebordered, distinct from the sternum, unnotched distally, and with a slight constriction at the base. The two notches marking this constriction resemble joint articulations; dark cuticle outlines each notch on BMNH I 8438. Both the pedipalp coxal endites and labium are setose. On IWCMS 1999.6, the pedipalp tarsus is modified into a cymbium, and bulb and sperm transmission structures can be seen; thus this specimen represents an adult male.

The walking leg coxae are rectangular in ventral view, and all about the same size. Precoxal triangles, sclerotized triangular extensions of the sternum pointing towards each coxa, are absent. The region between the coxae and lateral sternal margins is very clear in most specimens, so it is certain that precoxal triangles are absent in *Vectaraneus*. Trochanters 1–3, at least, appear not to be notched, i.e. have a notched limulus (e.g. IWCMS 1999.6). Trochanter 4 is less well preserved, so it is possible that a notch is present on this leg. Nearly complete walking legs are preserved on BMNH I 8440/I 8452, and their lengths suggest a formula of 4123. This specimen is, however, likely to be a juvenile, due to its smaller size relative to other specimens.

Cavities lined with drusy calcite at the anterolateral corners of the opisthosoma mark book-lung atria, immediately behind which about 12 lamellae are preserved as buff-brown calcite sheets, in BMBN 021960/1 (Text-fig. 4). The posterior margins of the book-lung regions are short and straight and it is probable that the book-lung openings occurred here. Fewer book-lung lamellae are preserved in IWCMS 1999.6. Book-lung openings can be seen at the lateral ends of the epigastric furrow in I 8438. On the holotype, two slit-like tracheal openings are present; the tracheal atria are connected and a distinct line or fold can be seen, so it is likely that a single, wide tracheal spiracle would be seen on the outer surface of the opisthosoma in the live animal. The spiracle is situated half-way between the epigastric furrow and the anterior spinnerets. A pair of large tracheae run to the anterior of the opisthosoma, diving into two trunks, and then tubules run on through the pedicel into the prosoma, as evidenced by a mass of fibrous calcite (Pl. 1, fig. 4). Within the large tracheal trunks, calcite replacement of spiral or annular thickenings can be seen in BMBN 021960/1 (Text-figs 4, 5A), and as annular markings on the tracheal walls in other specimens (Pl. 3, figs 5–6; Text-fig. 6). Such spiral thickenings occur in tracheae from a diverse range of spider families, and have been illustrated for uloborids, dictynids, dysderids, prodidomids, and anyphaenids by Lamy (1902, figs 4, 6, 9, 20–21, 27, and 52, respectively), and for anyphaenids by Ramírez (1995, fig. 12). The thickenings seem to occur only in larger tracheal tubes. There is no evidence of lateral tracheae in any *Vectaraneus* specimen; this suggests that none was present, given the excellent preservation of the median tracheae. However, the first branch of the median trachea occurs close to the epigastric furrow, and on I 8440/I 8452, it appears that the first branch occurs basally, contiguous with the origin of the main tracheal trunks, and becomes clearer in the region of the epigastric furrow.

Removal of the calcite replacement of the posterior opisthosomas of BMBN 021960 and In 17151 revealed the external moulds of the spinnerets and their setae embedded in the surrounding calcite matrix (Pl. 1, fig. 2; Text-figs 1–2, 5). The anterior spinnerets have a short basal segment which tapers distally; the terminal segment is short and conical. The anterior spinnerets are separated by about half their basal diameters in BMBN 021960. In other specimens they appear contiguous because the spinnerets are held close together. In modern spiders, even supposedly basal-contiguous spinnerets are actually separated by



TEXT-FIG. 9. *Vectaraneus yulei* gen. et sp. nov., upper Eocene, Bembridge Marls, Isle of Wight. Camera lucida drawing of paratype, BMNH I 8438. See text for abbreviations.

membrane, and may appear separated in a specimen with a distended opisthosoma, for example. For these reasons, the anterior spinnerets of *Vectaraneus* should be described as contiguous. The median spinnerets are visible only in BMBN 021960, where they are small and their bases contiguous; they lie between the anterior and posterior spinnerets. The posterior spinnerets are rather smaller than the anterior, but of a similar, tapering shape; the terminal segment is short and conical. The anal tubercle, seen in BMBN 021960/1, is distinct, and terminal in position. There is a raised, transverse lobe in front of anterior spinnerets in BMBN 021960/1, which may represent an ill-defined cribellum or colulus, but this feature is not evident in other specimens, nor is there any difference in setation in this area, so it probably represents a fold in the opisthosomal cuticle.

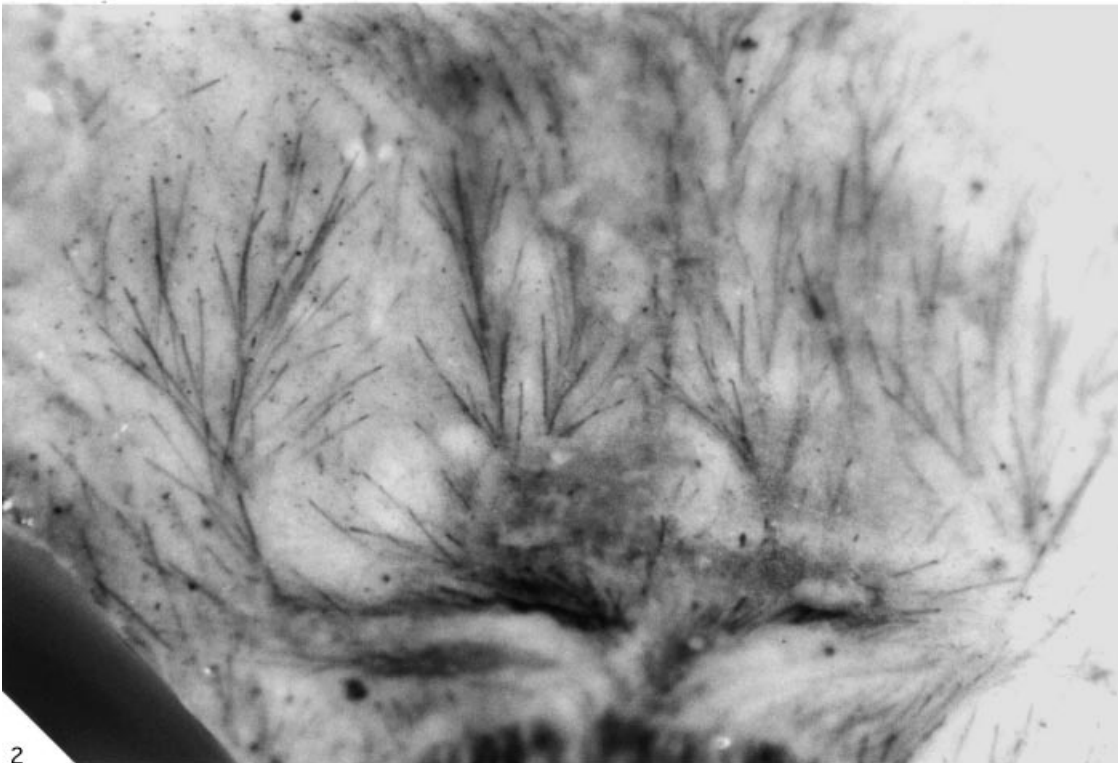
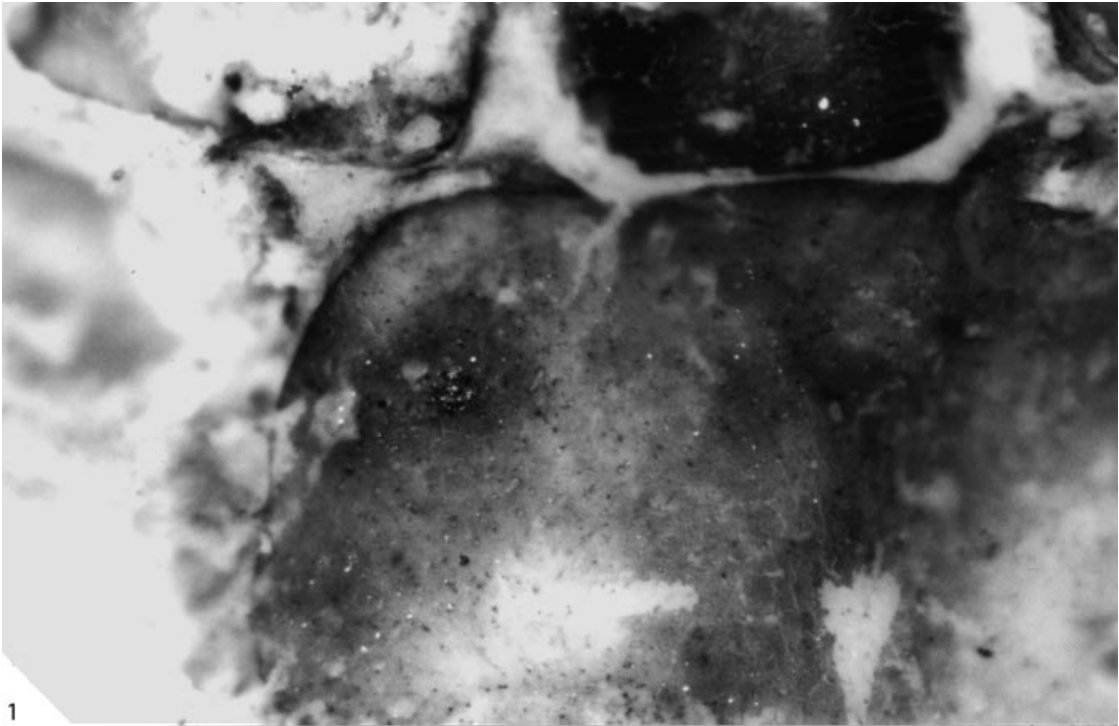
Text-figure 11 is a reconstruction of the ventral surfaces of male and female *Vectaraneus*.

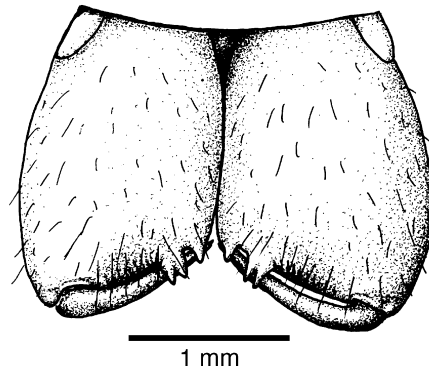
Eoatypus

The chelicerae of *Eoatypus* were figured by McCook (1888a, fig. 2; 1888b, fig. 2) as large and porrect, as in atypids. However, this is an artefact of fossils, as mentioned above. The chelicerae of *Eoatypus* are quite normal in size, and would have hung down beneath the anterior, cephalic part of the carapace. There may have been a distinct boss (articulation) at the anterolateral part of the dorsal edge of the chelicera, though the evidence is equivocal. By tilting the specimen and looking into the most anterior part of the carapace

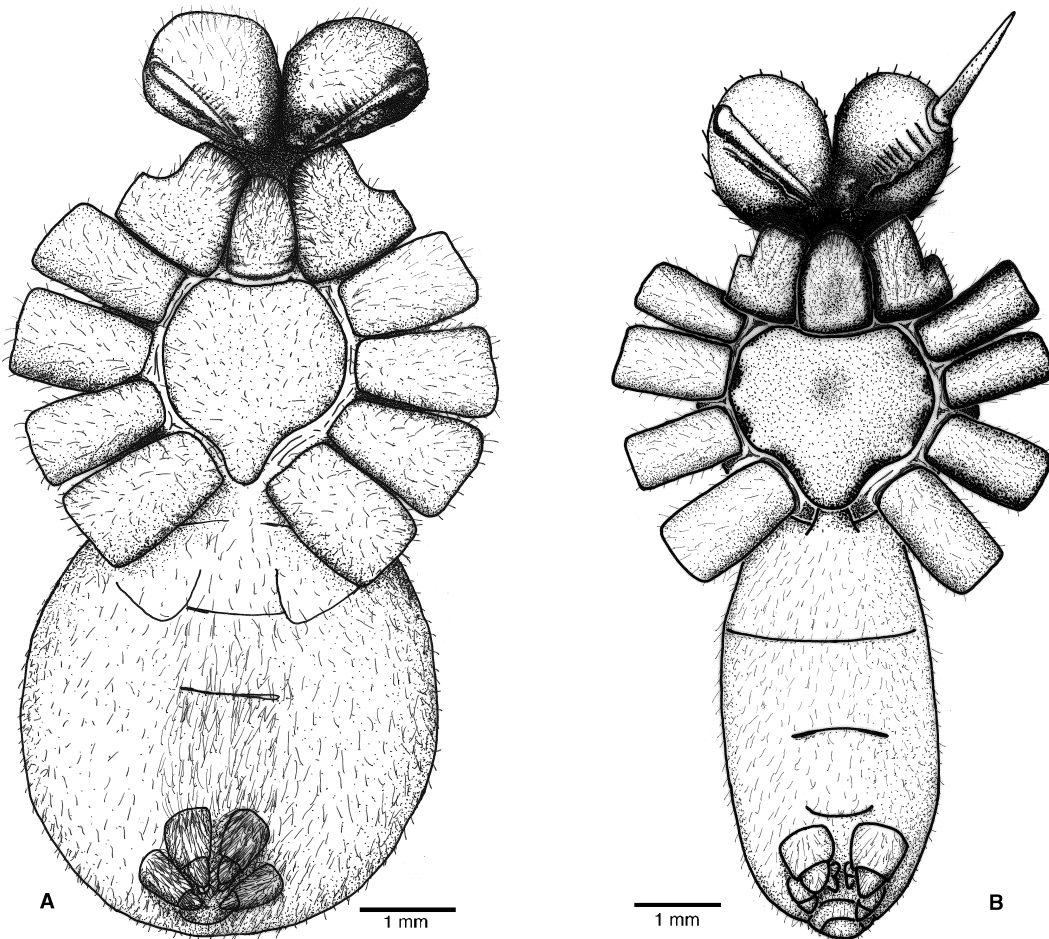
EXPLANATION OF PLATE 5

Figs 1–2. *Vectaraneus yulei* gen. et sp. nov., upper Eocene, Bembridge Marls, Isle of Wight; paratype, BMNH I 8438, under ethanol; $\times 75$. 1, detail of left anterolateral part of sternum and adjacent parts of labium and left pedipalp coxa; note cuticle with setal follicles, and slit sensillum (centre). 2, detail of setation around tracheal spiracle.





TEXT-FIG. 10. *Vectaraneus yulei* gen. et sp. nov., upper Eocene, Bembridge Marls, Isle of Wight. Reconstruction of chelicerae, anterior view.



TEXT-FIG. 11. A-B. *Vectaraneus yulei* gen. et sp. nov., upper Eocene, Bembridge Marls, Isle of Wight. Reconstruction of body, ventral view. A, ♀; B, ♂.

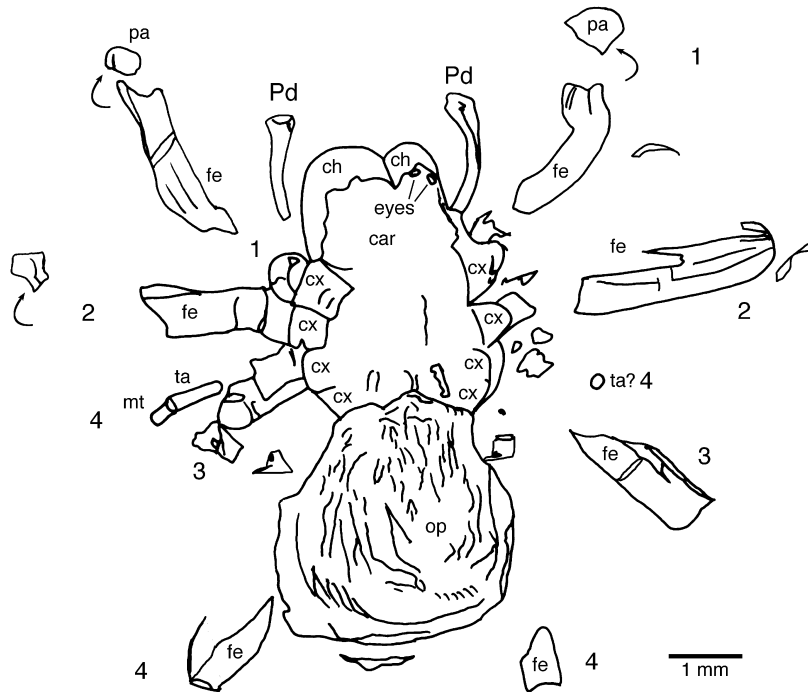
external mould, beneath the external moulds of the chelicerae, a slightly procurved row of four eyes, one diameter apart, and the impression of another row of eyes about two diameters in front of the posterior row, can be seen. If this is correct, then the spider is unlikely to be a mygalomorph because the eyes in this infraorder are generally grouped together on an ocular tubercle. The lateral edges of the carapace cannot be seen because they are obscured by parts of the coxae and trochanters of the walking legs. Text-figures 12 and 13 show the holotype specimen and a camera lucida drawing of it, respectively.

The pedipalp femora are slightly curved and the palps are not swollen; the distal thickenings remarked upon by McCook (1888*a, b*), Eskov and Zonshtein (1990), and Dunlop (1993) simply represent the joints between femur and tibia. Walking leg femora 1 and 2, and to a lesser extent 3, show a distinct break of slope about half-way along their length; this feature cannot be seen on femur 4 because only the distal parts of these femora are preserved. The break of slope looks superficially like a joint, but the distal part of the femur cannot be the patella because the reflexed knee occurs distal to it; in all spiders the patella either forms the knee or is distal to it. The change in slope is on the superior–prolateral surface of femora 1 and 2, and possibly superior–retrolateral in femur 3. In many spiders which hold their legs close up against the body, such as those living in a burrow, the prolateral surface of the anterior femora is curved and glabrous. Examples include the burrowing mygalomorph spiders such as migids, barychelids, idiopids, nemesiids, atypids, and ctenizids, and the araneomorph segestriids, amongst many others. The feature is rather better developed in *Eoatypus* than in these extant examples.

The opisthosoma is obviously wrinkled dorsally. Whilst this effect could be due, in part, to preservation, it is noteworthy that the *Vectaraneus* specimens described herein are not similarly affected. The style of wrinkling suggests a fairly thick cuticle which could hold the wrinkles without collapsing, to produce a good external mould. A soft opisthosoma, lacking sclerites, is characteristic of spiders, and allows distension of the opisthosoma following a large meal or the development of ova in females. In many spiders, the production of ova occurs once only in their lives, shortly followed by the death of the female, whilst in longer-lived species there may be a number of pregnancies, each accompanied by distension of the opisthosoma and subsequent contraction. Similarly, some spiders encounter prey infrequently; these enjoy short bursts of engorgement and opisthosomal distension, followed by long periods of starvation



TEXT-FIG. 12. *Eoatypus woodwardii* McCook, 1888, upper Eocene, Bembridge Marls, Isle of Wight; holotype, BMNH In 61271, dry; $\times 16$. See Text-figure 13 for explanation.



TEXT-FIG. 13. *Eoatypus woodwardii* McCook, 1888, upper Eocene, Bembridge Marls, Isle of Wight. Camera lucida drawing of holotype, BMNH In 61271. See text for abbreviations.

during which time the opisthosoma contracts. Such spiders need flexible, elastic opisthosomal cuticles which can withstand repeated stretching and relaxation. Many spiders show wrinkled, leathery (coriaceous) opisthosomal cuticles, e.g. *Xysticus*, a thomisid, which lives on open vegetation, encounters prey infrequently, and possibly needs a thick cuticle to help prevent desiccation; *Eresus*, which lives in a burrow and is long-lived; and *Ummidia*, a trapdoor spider. Note that these spiders are either inhabitants of open areas or long-lived (mainly mygalomorphs and some haplogyne araneomorphs). This hypothesis needs to be tested by a larger survey among spider families.

DISCUSSION OF VECTARANEUS

Respiratory organs

Review of respiratory organs in modern spiders. In his classic work, Lamy (1902) described the tracheal systems of all the main spider groups. Most araneomorphs show four narrow, unbranched (except at their ends) tracheal tubes: two median and two lateral. He recognized that the tracheae of all tracheate Araneae were homologous to each other and to the second pair of book lungs of more primitive spiders, and that they occurred on the third abdominal segment. He found no clear relationships between types of tracheal system and phylogeny (both simple and complex tracheae occur in a number of families, such as Uloboridae) and that biological reasons for the differences had not yet been established.

Purcell (1909) showed that the median tracheal trunks were derived from muscle apodemes whilst the lateral trunks were derived from pulmonary sacs. He considered that the similarities of tracheal systems in *Dysdera* and *Argyroneta* were due to convergence, the former being primitively anteriorly situated, the latter secondarily so. Purcell (1910) was more optimistic than Lamy about the phylogenetic use of spider tracheal systems, but he noted Lamy's (1902) emphasis on the inverse relationship between the number of

book-lung lamellae to tracheal size. For example, *Dictyna* has large tracheae but only four or five book-lung lamellae; *Segestria*, also with a large tracheal system, has 10–12 lamellae, whilst *Araneus* and *Agelena*, with normal, thin tracheae, have 60–70 book-lung lamellae.

Levi (1967) discussed adaptations of spider respiratory systems. Among other conclusions, he noted that if the respiratory organs of the third abdominal segment are large tracheae, then the spiracle moves posteriorwards in ontogeny, but then may move forward again. When tracheal systems are elaborate they are probably more efficient than lungs (more physiological data is necessary to support this observation). In small spiders, the book lungs of the second abdominal segment are weak or absent to prevent water loss; sometimes they are converted to tracheae too. Levi (1967) suggested that the tracheal system of the larger dysderoids was possibly inherited from their smaller ancestors. Sun-loving spiders may have more need of tracheae than those living in moist habitats. Aquatic and amphibious spiders have an elaborate tracheal system. Because these adaptations cross family boundaries, tracheal systems are no use as familial characters.

Forster (1980) proposed an elaborate scheme for the evolution of tracheal systems in Araneae. He supposed that the emergence and elaboration of tracheae correlated with smaller body size. The first tracheae were derived from the muscle apodemes of the posterior pair of book lungs; if anterior book lungs are transformed then it is always into tube tracheae, which do not involve muscle apodemes. Thus, he distinguished between (1) 'lamellae-tracheae progression', in which the book-lung lamellae are transformed into tube tracheae; and (2) 'booklung-apodeme progression', in which the book-lung apodemes produce the median trunks of the common type of tracheal system, the lamellae are lost, and the book-lung atria may be transformed into lateral tracheae. These two types involved further modifications, as outlined below.

(1) Dysderoid tracheae evolved from a cyatholipid type of posterior tube tracheae by the loss of the transverse (apodemal) connection and subsequent movement forwards of the tracheal spiracles. This hypothesis contrasts with the views of Purcell (1910), Kästner, (1929) and Levi (1967), who saw the anterior position of the dysderoid spiracles as primitive, and the embryological evidence of Winkler (1955) that the spiracles in *Dysdera* never migrate posteriorly. Forster (1980) described an evolutionary scenario to produce the tracheal arrangements seen in Telemidae, Leptonetidae and Ochyroceratidae. The paired nature of the tracheal trunks in these groups indicates their origin from book lungs rather than apodemes. Tracheal development of the first pair of book lungs occurs only after the second pair have evolved into tracheae and then only by lamellae-tracheae progression.

(2) *Thaida* has paired spiracles and short tracheal trunks but in *Filistata* the spiracles have merged to form a wide median spiracle. Generally, the spiracle migrates backwards but where this has not happened, the original book lungs are reduced (e.g. in Archaeidae, Sicariidae, and Pholcidae) or lost (Plectreuridae). Within 2 there are three separate progressions: (a) the apodemes fuse into a median lobe which then becomes vestigial, book-lung atria are converted to a simple pair of tracheae, and the spiracle rarely reaches the spinnerets (e.g. Palpimanoidea); (b) the apodemes become a pair of simple tubes, so that four simple tubes are present (e.g. most entelegyne families); (c) the apodemes retain their attachment function during backward migration, then either: (i) subdivide to produce a complex branched tracheal structure, or (ii) the attachment remains functional and simple tracheae gradually develop but are characteristically flattened anteriorly (e.g. Araneidae). In this progression, prosomal tracheation occurs only in the complex tracheal system c(i), and is usually accompanied by forward migration of the spiracle (e.g. *Argyroneta*, as shown by Crome 1953). Prosomal tracheation in lungless spiders involves tracheae from only one of the original pairs of book lungs.

An excellent study of spider tracheal systems, including a review of previous work, was provided by Bromhall (1987a).

Respiratory organs in Vectaraneus. In *Vectaraneus*, the second opisthosomal segment bears the usual pair of book lungs, and the third carries the tracheal spiracle. The wide tracheal spiracle is situated half-way between the epigastric furrow and the spinnerets; the spiracle leads to two large atria and tracheal trunks which run forwards, slightly diverging and then converging, to the pedicel. The first, large branches off the median trunks occur at the bases of the trunks. In the prosoma, there appear to be many small tubes (often

called tracheoles, they are neither homologous nor analogous to insect tracheoles) radiating forwards, as evidenced by fibrous calcite. There is no evidence for lateral tracheae. Because of their arrangement, with branches running forwards, and origin far behind the epigastric furrow, the preserved tracheae in *Vectaraneus* are considered to be median tracheae, i.e. apodemal in origin, rather than modified book lungs.

The arrangement of tracheal trunks and tubes in the fossil has no exact counterpart in any living spider. The arrangement is closest to that seen in the Dictynoidea *sensu* Forster (1970) (see Forster 1970, figs 1–22; Bromhall 1987a). Large tracheae occur in a number of extant spiders: Anyphaenidae, *Argyroneta*, Desidae, Dictynidae, Dysderidae, Hahniidae, Salticidae, and Segestriidae (Lamy 1902; Forster 1970; Bromhall 1987a). Anyphaenidae: Amaurobioidinae, *Argyroneta* and Desidae are aquatic and amphibious (intertidal) spiders, whose large tracheae (and other physiological adaptations such as a plastron and reduced heart rate in *Argyroneta*) correlate with the need to spend many hours breathing stored air under water. Other anyphaenids and Salticidae are active spiders, and the size of their tracheae has been correlated with this habit (Levi 1967). There has been no satisfactory explanation for the large size of the tracheae in Dictynidae or Hahniidae. In dictynids it might be correlated with their habit of living in exposed situations, such as at the top of bushes in arid environments; *Emblyna reticulata* (Gertsch and Ivie, 1936) is a common species on bushes in Death Valley, California (pers. obs.). Hahniids, however, are small, ground-living spiders of damp habitats (e.g. Opell and Beatty 1976). Their horizontal sheet webs condense water and make it available to the spider. Opell and Beatty (1976) referred to Levi's (1967) comments that small spiders are heavily sclerotized or remain in moist habitats to prevent desiccation. Possibly, the combination of lack of sclerotization and well-developed tracheal system in hahniids enables them to remain active in warm temperatures at small size. The tracheae of Dysderidae and Segestriidae are known to be derived from book lungs rather than apodemes (Purcell 1909); they may function differently from those of other spiders. Indeed, Bromhall (1987b) found that heart rates were lower in *Dysdera* and *Segestria* than in all other spiders he studied except *Argyroneta*. In *Dysdera*, an unusual alternation of faster and slower heart beat was attributed to pressure differences between prosoma and opisthosoma.

There are two, widely separated, tracheal spiracles in Dysderidae and Segestriidae, which correlates with the origin of the tracheae in these families from book lung atria rather than apodemes. In other families, a single spiracle is normal, although if the tracheae are large, as in *Anyphaena*, *Argyroneta*, and *Vectaraneus*, this is in the form of a wide cuticular fold concealing two distinct openings. In those spiders with a single tracheal spiracle, it is usually situated close to the spinnerets. In Desidae, the spiracle is a little way forward of the spinnerets; in hahniids, anyphaenids, and *Vectaraneus* it is around half way between the spinnerets and the epigastric furrow; in *Argyroneta* it is close to the epigastric furrow in adults, but more median in position in juveniles (Crome 1953).

Phylogenetic affinity

Forster (1970) placed Amaurobioididae, Anyphaenidae, Argyronetidae, Cybaeidae, Desidae, Dictynidae, and Hahniidae in the superfamily Dictynoidea, united by their large, branched, median tracheal trunks. He pointed out that in dictynoids in which tracheal systems extend into the prosoma, spiracles occur in a more anterior position than usual; this occurs in Anyphaenidae (which includes Amaurobioididae; see Platnick 1974; Ramírez 1995), Argyronetidae, some Desidae, and Hahniidae. The tracheal system of *Vectaraneus* falls into this category, demonstrating that it most likely belongs in this group of families. Hahniids are characterized by transversely arranged spinnerets, a feature not shared by *Vectaraneus*, so the possible phylogenetic affinity of the fossil is likely to be among Anyphaenidae, Argyronetidae or Desidae. Table 1 compares morphological features of *Vectaraneus*, Anyphaenidae, Cybaeidae (inc. *Argyroneta*), and Desidae (inc. *Desis*).

Desidae, as delimited by Forster (1970), is a diverse family of mainly intertidal spiders. Whilst the tracheal spiracle is wide and somewhat forward of the spinnerets, it is rarely more forward than one quarter of the distance from the spinnerets towards the epigastric furrow (Roth 1967b). Forster (1970) recognized two subfamilies: Desinae and Myroninae, which differ in that, among a number of characteristics, in

TABLE 1. Comparison of features of *Vectaraneus* gen. nov. with Anyphaenidae, Cybaeidae (*Argyroneta* in brackets), and Desidae (*Desis* in brackets). Italics denote characters in common with *Vectaraneus*.

Feature	<i>Vectaraneus</i>	Anyphaenidae	Cybaeidae [<i>Argyroneta</i>]	Desidae [<i>Desis</i>]
Chelicera: shape	<i>vertical</i>	<i>vertical</i>	<i>vertical</i>	commonly porrect
promarginal teeth	<i>3 (1+1 bifid)</i>	3–6	3	<i>toothed</i>
retromarginal teeth	<i>2 + carina/denticles</i>	5–9 minute	<i>denticles [2 teeth]</i>	<i>toothed</i>
furrow	<i>broad, ribbed</i>	narrow	narrow	<i>broad</i>
condyle	<i>distinct</i>	<i>distinct</i>	<i>distinct</i>	<i>distinct</i>
setal fringe	?	present	present [absent]	absent
Labium: shape	<i>longer than wide</i>	as long as wide	as long as wide	<i>longer than wide</i>
apex	<i>unnotched, rounded</i>	usually notched	<i>blunt</i>	rounded to <i>blunt</i>
basal notches	<i>present</i>	<i>present</i>	slight	<i>present</i>
Pedipalp coxa: shape	<i>rectangular</i>	<i>rectangular</i>	<i>rectangular</i>	elongate
scopula	<i>present</i>	<i>present</i>	<i>present</i>	<i>present</i> [absent]
serrula	<i>present</i>	<i>present</i>	<i>present</i>	absent
Legs: leg formula	<i>4123</i>	1423	<i>4123</i>	1423
ta claw tufts	<i>absent?</i>	lamellate	<i>absent</i>	<i>absent</i>
scopula	<i>absent</i>	dense	<i>absent</i>	weak
tr limulus	<i>unnotched</i>	notched	<i>unnotched</i> to slightly notched	notched [<i>unnotched</i>]
spines	<i>present</i> (fe,pa,ti,mt)	<i>present</i>	<i>present</i>	<i>present</i> [few on legs 1 and 2]
ta spines	<i>absent?</i>	<i>absent</i>	<i>absent</i>	present
Carapace: shape	<i>longer than wide</i>	<i>longer than wide</i>	<i>longer than wide</i>	<i>longer than wide</i>
fovea	?	longitudinal	longitudinal [weak]	distinct
Sternum: shape	<i>heart-shaped</i>	oval, apex pointed	<i>heart-shaped</i>	scutiform
precoxa triangles	<i>absent</i>	present	<i>absent</i>	<i>absent</i>
Opisthosoma: shape	<i>globular–ovoid</i>	ovoid	<i>globular</i>	ovoid
setation	<i>only normal setae</i>	plumose + normal setae	<i>normal</i> [+fine]	fine setae only
Tracheae: extent	<i>into prosoma</i>	<i>into prosoma</i>	<i>into prosoma</i>	opisthosoma only
spiracle position	<i>median</i>	<i>median</i>	posterior [anterior]	slightly anterior to spinnerets
spiracle width	<i>broad</i>	<i>broad</i>	narrow [wide, separate]	<i>broad</i>
median trunks	<i>large, thickened</i>	<i>large</i>	normal [<i>large</i>]	normal
lateral trunks	<i>absent?</i>	present	<i>absent</i>	present
Spinnerets: position	<i>subterminal</i>	terminal	<i>subterminal</i>	terminal
AS	<i>close together</i>	contiguous	<i>close together</i>	contiguous
MS	<i>very small</i>	large	<i>very small</i>	same size as AS
PS	<i>smaller than AS</i>	cylindrical	<i>smaller than</i> [equal to] AS	equal to or longer than AS
colulus/cribellum	<i>absent</i>	group of setae	<i>absent</i>	prominent colulus/cribellum
Anal tubercle	<i>distinct</i>	<i>distinct</i>	<i>distinct</i>	<i>distinct</i>
Total similarities with <i>Vectaraneus</i>	33	15	27[55]	13[12]

Myroninae the tracheal system extends into the prosoma, correct chelicerae are found only in males, and a colulus (in the form of a setose area) is present (in desines there may be a colulus or a cribellum, divided or undivided). In *Vectaraneus*, the tracheal spiracle is midway between the spinnerets and the epigastric furrow, and the following character states of *Vectaraneus* also differ from the usual state in Desidae (see Table 1 herein, and table 1 in Roth 1967*b* for characters of *Desis*): chelicerae not correct, pedipalp coxae, leg 1 and 2 spines present, tarsal scopula absent, median spinnerets smaller than anterior, colulus absent.

Platnick (1974) revised the North American Anyphaenidae, defining the family on the combination of the advanced position of the tracheal spiracle and the lamelliform claw tufts. Ramírez (1995) summarized more recent discussions on the relationships of the Anyphaenidae, and distinguished two alternative hypotheses based on reliable evidence. First, Forster's (1970) revised Dictynoidea, as mentioned above, was characterized on the shared possession of branched median tracheae, but he did not explain the exclusion from Dictynoidea of some other families with branched median tracheae, such as Salticidae, Thomisidae and Philodromidae. Bennett (1992) proposed secondary spermathecal pores as a synapomorphy of Dictynoidea, but these have not been found in Dictynidae and could be more widely distributed. The second hypothesis of anyphaenid relationships links the family with Clubionidae. Precoxal triangles were considered by Penniman (1985) as characteristic of the families Anyphaenidae, Clubionidae, Gnaphosidae, Liocranidae and Corinnidae. Coddington and Levi (1991) linked anyphaenids, clubionids and salticids on the shared absence (presumed loss) of cylindrical silk glands. However, as Ramírez (1995) has pointed out, some hahniids have precoxal triangles and cylindrical gland spigots are absent in cybaeids. He concluded that the problem of anyphaenid relationships will only be solved by analysis of the monophyly of the Dictynoidea, on the one hand, and Dionycha (where Coddington and Levi 1991, fig. 2, had them), on the other.

Vectaraneus shows a number of features consistent with identification as an anyphaenid (see Table 1). The large median tracheal trunks arising from a wide, medially situated spiracle are characteristic of anyphaenids. The arrangement of tracheae, with a large branch arising close to the base of the primary median trachea, is also similar to the anyphaenid arrangement. However, no tarsal claw tufts, the other diagnostic feature of Anyphaenidae, can be seen on *Vectaraneus* (Pl. 3, fig. 2), although absence of evidence should not be taken as evidence of absence. Of the three anyphaenid superfamilies distinguished by Ramírez (1995), Malenellinae, Anyphaeninae, and Amaurobioidea, the tracheal system of *Vectaraneus* most closely resembles Anyphaeninae, a subfamily distinguished by the most forwardly advanced tracheal spiracle (midway or closer to the epigastric furrow). However, other character states of *Vectaraneus* differ from those in anyphaenids (Table 1), including: no precoxal triangles, apparent lack of lateral tracheae, heart-shaped sternum, no leg scopulae, rounded opisthosoma (in most specimens), and lack of bristly setae (Roth and Brame 1972, fig. 4; = plumose setae of Lehtinen 1967, fig. 8).

The European Water Spider, *Argyroneta aquatica*, has been placed variously in the subfamily Cybaeinae within Agelenidae (e.g. Grothendieck and Kraus 1994), a subfamily which is commonly raised to family status (Bennett 1991; Platnick 1993, 1997), in a monotypic subfamily Argyronetinae of Agelenidae, or family Argyronetidae, generally allied to Cybaeinae(-idae) (e.g. Platnick 1993). Lehtinen (1967) placed Argyronetinae and Cybaeinae in Dictynidae in his superfamily Amaurobioidea, on the basis of perceived similarities in genitalia; Forster (1970) put Argyronetidae and Cybaeidae in Dictynoidea on the basis of their tracheal systems. However, Forster (1970) disagreed with most other authors on the close relationship between *Argyroneta* and Cybaeidae, preferring a closer alliance of *Argyroneta*, *Amaurobioidea* and Anyphaenidae. He pointed to the similar tracheal system of these three taxa: median tracheae extending into prosoma and lateral tracheae with two trunks and tracheoles. Ramírez (1995) concluded, from a study of the development of tracheal systems in anyphaenids, that the second lateral branch is in reality the first branch of the median trachea. Grothendieck and Kraus (1994) argued that, apart from specializations for aquatic life, *Argyroneta* was easily accommodated in Cybaeinae. Indeed, there is justification in including *Argyroneta* in Cybaeinae(-idae) since a monotypic family Argyronetidae, carries less phylogenetic information.

Bennett (1991) reviewed the family Cybaeidae in North America. These small to medium-sized, litter-dwelling spiders are common in damp Pacific forests of California to British Columbia. Very few species of *Cybaeus* occur in the Appalachians, where coelotine agelenids generally replace them ecologically (conversely, in the west, coelotines are rare). A number of cybaeid genera occur in western states, three have been described from Japan, one from Venezuela, and *Cybaeus* has Eurasian representatives (including the type species, *C. tetricus*) as well as North American. Bennett (1991) found no evidence in support of the monophyly of the family, but some characters linked most of the genera and, in the absence of evidence placing these or other described cybaeids elsewhere, he considered the family a usable group, and this conclusion was followed by Platnick (1997). Table 1 summarizes the morphological features of Cybaeidae.

From the point of view of the phylogenetic placement of *Vectaraneus*, could it be an *Argyroneta* or cybaeid? *Vectaraneus* differs from *Argyroneta* in lacking a felt of fine hairs forming a plastron over the opisthosoma, and the spiracle is not so far forward in *Vectaraneus* as in *Argyroneta*. Both of these features are related to the aquatic habitat of *Argyroneta*, and its need to carry and breathe air under water. The tracheal system of *Argyroneta* shows some similarities with *Vectaraneus*; the wide tracheal spiracle and large median trunks, for example; but there are differences. Apart from the more forward position of the spiracle in *Argyroneta*, this spider has many fine lateral tracheal tubes (Crome 1953, fig. 13). It is, of course, possible that the absence of lateral tracheae in *Vectaraneus* is a preservational artefact, as mentioned above.

Some species of modern dictynoids are difficult to place in generally recognized families. *Mizaga* Simon, 1898, is a genus of cribellate, littoral spiders from west Africa and the Mediterranean which has been placed in Desidae (Fage 1925, as *Desidiopsis*), Agelenidae (Simon 1898; Roth 1967a), and Dictynidae, Tricholathysinae (Lehtinen 1967; a placement followed by Dippenaar-Schoeman and Jocqué 1997 and Platnick 1997). *Swainsia* Marples, 1964, known from a single male collected on Swains Island, South Pacific, was placed in Agelenidae by its describer and transferred to Dictynidae, Litisedinae by Lehtinen (1967), who commented (p. 353) that this subfamily ‘seems to be the dictynid equivalent of the Desinae, as far as ecological adaptation is concerned, and thus the external similarity of these two groups is noticeable’. The widespread littoral spider genus *Desis* Walckenaer, 1837, has been placed in Agelenidae by many authors, and in its own family Desidae Pocock, 1895. Desidae was redefined by Roth (1967b), and later expanded by Forster (1970). Lehtinen (1967), on the other hand, placed subfamily Desinae in his redefined Amaurobiidae. Jocqué (1994) and Dippenaar-Schoeman and Jocqué (1997) have commented on the limits of Desidae, which seems to belong in Dictynoidea. The genera just discussed share the commonality of a littoral habitat. Therefore, it is perhaps not surprising that they are difficult to place, since their adaptations for life in this habitat (e.g. large tracheal system with spiracle in an anterior position) appears as a deviation from the normal pattern of recognized families. It is likely that there have been parallel colonizations of the littoral habitat by members of a number of spider families (see later).

Fossil spiders referred to Argyroneta

Von Heyden (1859) described a fossil spider from the Miocene Brown Coal of Grube Stöschen, near Linz am Rheine, Germany, as *Argyroneta antiqua*, placing it in that genus on account of its general appearance (and, presumably, its preservation in a swampy environment), rather than on the basis of any characteristic morphological features, which are lacking in the fossil. Heer (1865, 1872, 1876) described a collection of spiders from the Miocene of Oeningen (Öhningen), on the border of Switzerland and Germany. A particularly long-legged form he referred to *Argyroneta*, and named *Argyronecta?* [*sic*] *longipes*. In regard to this specimen, Heywood (footnote in Heer 1876, p. 11) commented: ‘Unfortunately the two specimens which Prof. Heer received are not sufficiently well preserved for certain determination. The comparative lengths of the legs, the thin filiform palpi, and the rounded form of the sides of the cephalothorax are in favour of it being referred to *Argyronecta*; but the cephalothorax is less prominent in front than in the existing species. A similar form of cephalothorax and legs also occurs in *Tegenaria*. According to Thorell [1870, see below] this species does not belong in *Argyronecta*, but seems to form a distinct genus’. Thorell (1870) created the new genus *Elvina*, diagnosed by the palps being thicker than the legs, not for Heer’s

specimen, but for the one described by von Heyden (1859). Thorell (1870, p. 224) suggested that *Argyroneta antiqua* von Heyden, 1859, probably belonged in Tubitelariae (a name no longer in use for a group of spiders which do not fall easily into any other category, including Agelenidae, Gnaphosidae, Clubionidae, Urocteidae, Filistatidae and Dysderidae), and possibly (Thorell's emphasis) in Agelenidae: Argyronetinae. As for *A. longipes* Heer, 1865, Thorell (1870) was certain that it did not belong in *Argyroneta*.

Bertkau (1878) described a collection of fossil spiders and a milliped from the Brown Coal of Rott, including 19 specimens he referred to *Argyroneta antiqua*, ten (including von Heyden's holotype) from the Kieselschiefer ('flint-slate') and nine from the Blätterkohle ('leaf-coal'). He gave a detailed description of the species, described the heart-shaped sternum, and discussed the nature of prominent parallel bands ('Längstreiffen') on the opisthosomas of the Kieselschiefer specimens, concluding that these represented a prominent tracheal system. He concluded that the new specimens were conspecific with the holotype of *A. antiqua* von Heyden, 1859, and that the species belonged in *Argyroneta* but differed from *A. aquatica* principally in that the tracheal spiracle was more posterior in position than in the type species. He was quite familiar with *Argyroneta*, and with spider tracheal systems in general, having published on spider respiratory organs a few years earlier (Bertkau 1870). Thus, Bertkau (1878, p. 359) clearly understood the importance of his conclusion that the fossils were an example of an evolutionary missing-link: 'Eine Gewissheit in dieser Frage wäre allerdings von hohem Interesse, da mir der gegenwärtige Fall für die Descendenztheorie besonders lehrreich zu sein scheint.'

Petrunkevitch mentioned Bertkau's (1878) work briefly in his 1958 paper, to confirm his earlier-expressed doubts regarding the generic affiliation of *Argyroneta antiqua* von Heyden, 1859, but not in his 1946 detailed study of a specimen of *A. antiqua* from the Brown Coal of Rott held in the American Museum of Natural History (AMNH 26275). In the 1946 study, Petrunkevitch noted that if von Heyden's (1859) measurements of the leg lengths were correct, making the leg formula 1234, then the holotype of *A. antiqua* could not belong in *Argyroneta*, which has a leg formula of 1423. The detailed description of the AMNH specimen given by Petrunkevitch (1946) accords with that of Bertkau (1878). It is possible that AMNH 26275 is one of the specimens studied by Bertkau, and that Petrunkevitch had forgotten Bertkau's (1878) paper in 1946. The 19 specimens described by Bertkau (1878) seem to have been distributed to a number of museums. There are two Blätterkohl specimens in The Natural History Museum, London (numbered 59627 and In 39930, both labelled as purchased from R. Damon, March 1877); and a drawer-full in the George Stutz Collection in the Los Angeles County Museum of Natural History, including one specimen (LACM 3086) figured by Furst (1959, 1970).

Bertkau (1878) considered the Rott specimens to be conspecific with *Argyroneta antiqua* von Heyden, 1859. In his study of AMNH 26275, Petrunkevitch (1946) showed that this specimen was not conspecific with the holotype of *A. antiqua*. My studies of the latter (see below) show that it is not an *Argyroneta*, and of BMNH specimens 59627 and In 39930 indicate they are not conspecific with *A. antiqua*. Bertkau's specimens, however, are close to the extant *Argyroneta aquatica*, differing, as Bertkau (1878) mentioned, by the more posterior position of the tracheal spiracle. In this, they resemble *Vectaraneus*. However, *Vectaraneus* appears to lack the plastron of fine hairs on the abdomen and possibly also the long hairs on the posterior two legs (the relevant podomeres are poorly preserved in *Vectaraneus*), both of which occur in the Bertkau specimens.

Mode of life

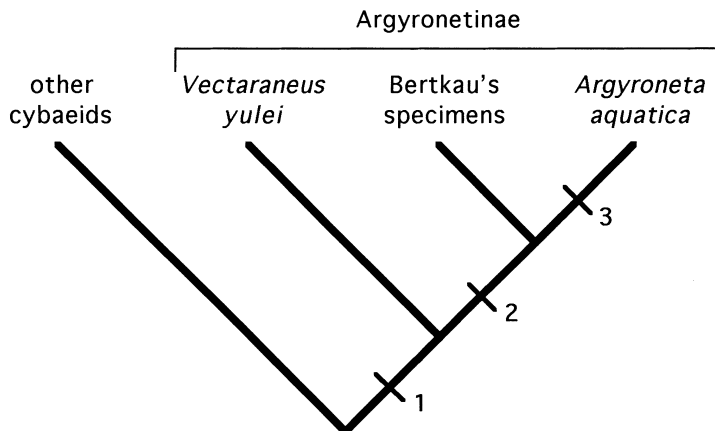
Large tracheae are characteristic of active spiders and those with aquatic or amphibious habits, and correlate with a reduced number of book-lung lamellae. Bromhall (1987b, fig. 2) demonstrated the negative correlation between extent of tracheation and heart rate in spiders. The families Desidae and Anyphaenidae contain both marine littoral genera (e.g. *Desis*, *Amaurobioides*) and active hunters on foliage (e.g. *Anyphaena*, *Laestrygones*). It is not clear whether (1) the littoral genera evolved from active hunters or (2) *vice versa*, (3) both types evolved separately from a common ancestral habit, or (4) whether, indeed, there is any congruity between modes of life and desid and anyphaenid phylogeny, but the well developed tracheal system appears to be advantageous for both modes of life. Forster (1970) noted the

correlations between large tracheal trunks extending into the prosoma, forward position of the tracheal spiracle, and an aquatic or semi-aquatic mode of life. The European Water Spider, *Argyroneta*, differs from other cybaeids in the forward position of the wide tracheal spiracle and the large tracheal trunks which divide into many tracheal tubules within the prosoma. *Vectaraneus* follows this pattern, so might be expected to have had an amphibious or aquatic mode of life.

Evidence for habitat is provided by sedimentology and associated biota, and both aquatic (lacustrine) and terrestrial (woods and meadows) are possible; fossil insects from both habitats have been recorded (Jarzembowski 1980; McCobb *et al.* 1998). Possibly, the Bembridge spider was aquatic and is preserved in its life habitat; however, it is likely that, under normal circumstances, an aquatic spider would be less prone to be killed by drowning than a terrestrial spider. Nevertheless, aquatic animals such as crustaceans and molluscs occur as fossils in the Bembridge Marls (McCobb *et al.* 1998), including *Branchipodites* on the same slab as BMBN 021960/1. Their presence in the Insect Bed suggests that abnormal conditions, such as a change in water chemistry, were responsible for the death and preservation of the biota. *Vectaraneus* lacks the specific adaptations for a fully aquatic mode of life, as seen in *Argyroneta*, e.g. a plastron. Nevertheless, there are many amphibious spiders known in both freshwater and marine habitats. In a review of spiders inhabiting the littoral zone, Roth and Brown (1976) referred to species belonging to eleven families: Agelenidae, Anyphaenidae, Barychelidae, Clubionidae, Desidae, Dictynidae, Gnaphosidae, Hahnidae, Linyphiidae, Lycosidae, and Salticidae. These species are able to withstand periodic flooding by the use of web stretched across a rock or vacated shell retreat. Indeed, these authors commented that it is surprising that not more spiders have exploited this habitat, with its abundance of crustacean food. Many lycosoids live in swampy freshwater habitats where they walk on water, dive for food and, in the case of *Pirata* spp., construct a subaerial, tubular retreat with the entrance submerged beneath the water surface.

CONCLUSIONS

It is evident from the foregoing discussion, and especially from the comparison of features in Table 1, that *Vectaraneus* is a cybaeid which exhibits a state of development of its tracheal system between that of the European Water Spider, *Argyroneta aquatica*, and other cybaeids. *Vectaraneus* could be described as a 'missing link' in the Darwinian sense, but it cannot be an ancestor to *Argyroneta* because of its autapomorphies. Text-figure 14 shows the hypothesized relationship between *Argyroneta aquatica*,



TEXT-FIG. 14. Cladogram showing hypothesized relationship between *Vectaraneus yulei*, *Argyroneta aquatica*, Bertkau's specimens, and other Cybaeidae. Characters at node 1 defining Argyronetinae: enlarged tracheal trunks running into prosoma, and wide tracheal spiracle situated well forward of base of spinnerets; at node 2 (Bertkau's specimens + *A. aquatica*): dense opisthosomal pilosity (plastron), and long setae on legs 3 and 4; and at node 3 (*A. aquatica*): tracheal spiracle close to epigastric furrow in adult.

Vectaraneus, the specimens described by Bertkau (1878), and other Cybaeidae. Redescription of Bertkau's specimens is clearly the next step in the study of the relationships of Argyronetinae; this is planned but is beyond the scope of the present study.

The anteriorly positioned tracheal spiracle (a feature independently acquired in several amphibious spiders), large tracheal system, systematic placement, and palaeoenvironmental evidence all points towards the habitat of *Vectaraneus* being close to water, and to the spider having been amphibious in its mode of life.

SYSTEMATIC PALAEONTOLOGY

Order ARANEAE Clerck, 1757
 Suborder OPISTHOTHELAE Pocock, 1892
 OPISTHOTHELAE *incertae sedis*
 Genus EOATYPUS McCook, 1888

Type species. Eoatypus woodwardii McCook, 1888, by monotypy.

Eoatypus woodwardii McCook, 1888

Text-figs 12–13

- 1888a *Eoatypus woodwardii* McCook, p. 200, figs 1–2
- 1888b *Eoatypus woodwardii* McCook; McCook, p. 367, figs 1–2
- 1890 *Eoatypus woodwardii* McCook; McCook, p. 456, figs 383–384
- 1955 *Eoatypus woodwardii* McCook; Petrunkevitch, p. P136, fig. 100,2
- 1980 *Eoatypus woodwardii* McCook; Jarzembowski, p. 240
- 1984 *Eoatypus woodwardii* McCook; Selden, p. 4
- 1990 *Eoatypus woodwardii* McCook; Eskov and Zonshtein, p. 326
- 1993 *Eoatypus woodwardii* McCook; Dunlop, p. 3, fig. 8

Type and only known specimen. BMNH In 61271, The Natural History Museum, London, from upper Eocene Bembridge Marls ('Insect Bed') of Gurnard Bay (= Gurnet Bay), Isle of Wight, England.

Emended diagnosis. Opisthothele spider with femora 1–3 with concave superior–prolateral surfaces showing change of plane about half length of podomere; wrinkled opisthosomal cuticle.

Description. All measurements approximate. Body length (inc. chelicerae) 7.33; carapace length 3.52, width 2.86. Four eyes present in wide, slightly procurved row, one diameter apart; another row anterior to these can just be made out on the specimen. Pd fe 1.42, fe1 3.05, fe4 3.24. Superior–prolateral surfaces of pedipalp and leg 1–3 femora concave, with distinct change in plane of surface about half length of podomere. Opisthosoma 3.81 long, 3.33 wide, wrinkled.

Remarks. McCook (1888a, b) named this spider *Eoatypus woodwardii*, but subsequent authors spelt the trivial name 'woodwardi'. According to *International Code of Zoological Nomenclature* article 33.4 (International Commission on Zoological Nomenclature 1999): 'The use of the genitive ending -i in a subsequent spelling of a species-group name that is a genitive based upon a personal name in which the correct original spelling ends with -ii, or vice versa, is deemed to be an incorrect subsequent spelling, even if the change in spelling is deliberate'. Thus, the specific name *Eoatypus woodwardii* is used here.

McCook saw this specimen during a visit to the British Museum (Natural History), London, in 1887,

and the keeper, Henry Woodward, later sent plaster and wax casts to McCook for further study. His (1888*a, b*, 1890) figures and subsequent copies (e.g. Petrunkevitch 1955) are of these casts, not the original specimen. Dunlop's (1993) figure is taken from the original, but is a sketch and is not accurate.

Eoatypus clearly differs from *Vectaraneus*, which occurs in the same beds, by the distinctly concave superior–prolateral surfaces of the anterior femora, and the wrinkled opisthosoma. The eyes apparently in two, wide rows suggests an araneomorph spider, but this is not confirmed by other characters. *Eoatypus* is not a mesothele because of the lack of dorsal opisthosomal sclerites. It is therefore placed as Opisthothelae *incertae sedis*.

Infraorder ARANEOMORPHAE Smith, 1902

ARANEOMORPHAE *incertae sedis*

Genus ELVINA Thorell, 1870

Type species. Argyroneta antiqua von Heyden, 1859.

Elvina antiqua (von Heyden, 1859)

Text-fig. 15

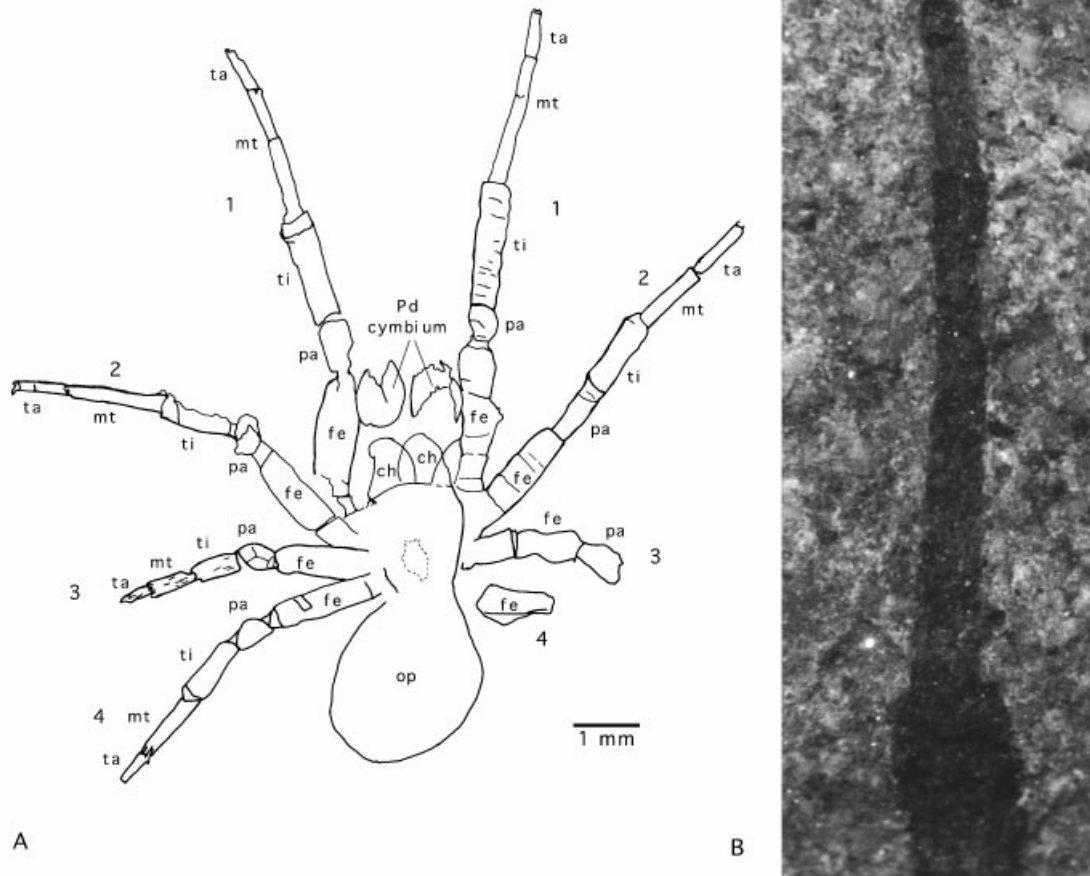
- 1859 *Argyroneta antiqua* von Heyden, p. 1, pl. 1, fig. 12.
 1870 *Elvina antiqua* (von Heyden, 1859); Thorell, p. 224.
non 1878 *Argyroneta antiqua* von Heyden; Bertkau, p. 352, pl. 5, fig. 1a–c.
non 1946 *Argyroneta antiqua* Heyden; Petrunkevitch, p. 19, fig. 80.
non 1955 *Argyroneta antiqua* van Heyden [*sic*]; Petrunkevitch, p. P152, fig. 109,5.
non 1958 *Argyroneta antiqua* Heyden; Petrunkevitch, pp. 358, 387.
 1967 *Argyroneta antiqua* [*sic*] C. von Heyden; Roth (1967*b*), p. 7.
 1980 *Argyroneta antiqua* Heyden; Morris, p. 28.
 1993 *Elvina antiqua* (von Heyden, 1859); Selden, p. 315.

Type and only known specimen. BMNH 58825, The Natural History Museum, London, from Miocene Brown Coal of Grube Stöschen, near Linz am Rhein, Germany.

Emended diagnosis. Araneomorph spider with leg formula 1243; tarsi short; oval abdomen.

Description of holotype and only known specimen, BMNH 58825. All measurements approximate. Mature male (swollen pedipalp tarsus). Abdomen oval. Leg formula 1243; legs of medium length cf. body. Tarsi short cf. metatarsi. Approximate lengths: body (inc. chelicerae) 5.1; abdomen 2.7 (width 2.1); carapace 1.7; chelicerae 0.8; pd ta 1.0; fe1 2.0, pa1 0.7, ti1 1.8, mt1 2.1, ta1 0.79; fe2 \geq 1.4, pa2 0.7, ti2 1.3, mt2 1.3, ta2 0.9; fe3 \geq 1.4, pa3 0.6, ti3 0.7, mt3 0.7, ta3 0.5; fe4 \geq 1.5, pa4 0.7, ti4 1.1, mt4 1.2, ta4 \geq 0.5.

Remarks. Von Heyden (1859) placed this specimen in the European Water Spider genus *Argyroneta* on the basis of its habitus (i.e. general appearance) and, presumably, consideration of its preservation in swamp conditions as well. Petrunkevitch (1946) remarked that the segmentation of the legs was not visible; since it clearly is, it can be concluded that he did not see the specimen. Von Heyden (1859) gave a leg formula of 1234 or 1243; Petrunkevitch (1946) pointed out that the leg formula of the modern *Argyroneta* is 1423 (the fourth legs in this genus are large, possibly modified for swimming). Thus, von Heyden's specimen cannot be placed with certainty in the genus *Argyroneta*. Indeed, little can be said about this specimen except that it is a spider, and most likely an araneomorph as evidenced by the large palpal cymbium of this adult male specimen. Thorell (1870) provided an alternative generic name, *Elvina*, which is available for this specimen.



TEXT-FIG. 15. A-B. *Elvina antiqua* (von Heyden, 1859), holotype, BMNH 58825. A, camera lucida drawing of complete specimen. B, right leg 1 distal ti, mt, and ta, showing mode of preservation; $\times 34$.

Superfamily DICTYNOIDEA Simon, 1874
 Family CYBAEIDAE Simon, 1898
 Subfamily ARGYRONETINAE Menge, 1869

Emended diagnosis. Cybaeidae with enlarged tracheal trunks running into prosoma; wide tracheal spiracle situated well forward of base of spinnerets.

Included genera. *Argyroneta* Latreille, 1804; *Vectaraneus*, gen. nov.

Remarks. With the recognition of the sister relationship of *Vectaraneus* and *Argyroneta* Latreille, 1804 + Bertkau's specimens, the name Argyronetinae Menge, 1869, previously used by many authors for a monotypic subfamily or family, is available for this clade. *Argyronecta?* [*sic*] *longipes* Heer, 1865, does not belong here (see Thorell 1870, p. 224). The specimens described by Bertkau (1878) belong in this subfamily, possibly as a new genus.

Genus ARGYRONETA Latreille, 1804

Type and only species. *Argyroneta aquatica* (Clerck, 1757).

Emended diagnosis. Argyronetine with wide tracheal spiracle close to epigastric furrow in adult; abdomen with dense pile of fine hairs forming plastron; legs 3 and 4 with long hairs.

Remarks. The specimens described by Bertkau (1878) may belong in this genus (they differ in the more posterior position of the tracheal spiracle in the adult), but a redescription of them is necessary before their systematic placement can be confirmed.

Genus VECTARANEUS gen. nov.

Derivation of name. Latin, *Vectis*, the Isle of Wight; and *araneus*, a spider.

Type species. *Vectaraneus yulei* sp. nov. (see below).

Diagnosis. Argyronetine with wide tracheal spiracle situated midway between spinnerets and epigastric furrow; lacking plastron; cheliceral furrow with transverse ridges; large, bifid tooth (fissidentate) and smaller tooth proximally at proximal end of cheliceral promargin, retromargin with two teeth proximally and carina (possibly row of contiguous denticles) running, and fading, towards base of fang.

Remarks. *Vectaraneus* is placed in Cybaeidae, Argyronetinae, on the basis of the medial position of the tracheal spiracle, between the position in most cybaeids and that in *Argyroneta* (and in a similar to position to that in juvenile *Argyroneta* (Crome 1953, figs 51–54), and the greater similarity of features with that family than others which show forwardly positioned spiracles: Anyphaenidae, Hahnidae, and (to a lesser extent) Desidae (Table 1).

Vectaraneus yulei sp. nov.

Plates 1–5; Text-figs 1–9

Derivation of name. After Andrew Yule, prolific collector of Isle of Wight fossils.

Holotype. BMBN 021960 part and 021961 counterpart (ventral and dorsal) respectively, preserved as external mould with some adhering organic material and internal fine replacement by calcite, from upper Eocene Bembridge Marls ('Insect Bed') of Thorness Bay, Isle of Wight, England, collected by E. A. Jarzembowski, deposited in the Booth Museum of Natural History, Brighton, England.

Paratypes. IWCMS 1999.6, Isle of Wight Museum of Geology, Sandown, Isle of Wight; BMNH In 17151, BMNH I 8438, BMNH I 8440 and I 8452 (part and counterpart), The Natural History Museum, London. All from upper Eocene Bembridge Marls ('Insect Bed') of Gurnard Bay (except IWCMS 1999.6 which is from Thorness Bay), Isle of Wight, England.

Diagnosis. As for the genus.

Description of BMBN 021960/1. Mature female? Posterior border of carapace straight; posterolateral corners of carapace curved, dorsal side of posterolateral area of carapace slightly concave; remainder of carapace not visible. Sternum heart-shaped, wider than long (2.2 × 1.9), anterior border slightly procurved, posterior border produced strongly between leg 4 coxae, lateral edges slightly scalloped; surface convex apart from median longitudinal depression just anterior to midpoint; surface covered with short setae. Labium large, longer than wide, slightly tapering to the anterior, slightly notched at the base. Chelicera large (1.9 long), robust; cheliceral furrow broad, shallow

(undefined) with transverse ridges; large, double-pointed tooth with smaller subsidiary tooth at proximal (mesial) end of cheliceral furrow, retromargin with a row of teeth. Pedipalp coxa large, subrectangular. Leg coxae subequal in size. Opisthosoma 4.5 long (as long as prosoma inc. chelicerae), 2.2 wide, subparallel-sided, covered with long, fine setae. Book lungs with about 12 lamellae visible and atria in anterior part present at anterolateral corners of opisthosoma. Wide tracheal spiracle situated approximately half-way between book-lungs and spinnerets. Spiracle leads to pair of large tracheae running anteriorly to anterior of opisthosoma, diving into two trunks within opisthosoma (secondary branch arising at *c.* one-third of length of major trachea and running alongside to pedicel), tubules running through pedicel into prosoma. Both primary and secondary tracheae with cuticular reinforcements. Anterior spinnerets with terminal segment probably short and conical, separated by about one-half basal diameter. Median spinnerets small, contiguous. Posterior spinnerets smaller than anterior, with terminal segment probably short and conical. Anal tubercle large, terminal. Raised, transverse lobe in front of anterior spinnerets (cuticular fold or ill-defined cribellar/colular area).

Description of IWCMS 1999.6. Mature male. Ventral surface only preserved. Sternum heart-shaped, slightly longer than wide (2.18×2.07), anterior border slightly procurved, posterior border produced strongly between leg 4 coxae, lateral edges slightly scalloped; surface convex. Labium large, longer than wide (0.09×0.49), slightly tapering to the anterior, slightly notched at the base. Chelicera 1.64 long, robust; cheliceral furrow broad, shallow (undefined) with transverse ridges; large, double-pointed tooth with smaller subsidiary tooth at proximal (mesial) end of cheliceral furrow, retromargin with two teeth and a carina (possibly serrate). Pedipalp coxa large, subrectangular, serrula present on mesial edge; parts of tibia and palp cymbium and bulb preserved. Leg coxae approximately equal in size (0.42). Tr1 0.65, fe4 2.89, ti4 ≥ 3.00 . Opisthosoma 4.74 long, 3.43 wide, oval, densely setose, especially ventrally. Remains of book lungs occupy anterolateral corners of opisthosoma; extending about one-quarter opisthosoma length posteriorly. Wide tracheal spiracle situated approximately half-way between book-lungs and spinnerets. Spiracle leads to pair of large tracheae. Anterior spinnerets with terminal segment short and conical. Posterior spinnerets smaller than anterior, with terminal segment short and conical.

Description of BMNH I 8440 (part) and I 8452 (counterpart). Immature specimen. Carapace approximate length 2.47, width 3.10. Sternum: mostly internal mould preserved. Labium bell-shaped, about as long as wide. Chelicera vertical, boss (condyle) at anterolateral corner. Pedipalp coxa longer than wide. Podomeres: pa1 ≥ 0.56 , ti1 1.75, mt1 1.75, ta1 0.89; fe4 ≥ 2.22 , pa4 0.89, ti4 1.5, mt4 1.5, ta4 1.06. Opisthosoma 2.61 long, 2.50 wide. Tracheae maximally 0.28 wide.

Description of BMNH In 17151. Immature specimen. Carapace not preserved. Sternum heart-shaped, 1.61×1.61 (with fibrous calcite in posterior part). Labium longer than wide, slightly tapering anteriorly. Chelicera with promarginal bifid tooth, retromarginal tooth row, ridged furrow, and partial mould of fang visible on left side. Pedipalp coxae slightly longer than wide, serrula present on mesial edge, endites setose. Cx1 1.11. Parts of other coxae, fe1, fe2, mt/ta1, mt/ta2 also preserved. Opisthosoma full of botryoidal calcite; anterior spinnerets and one other pair (presumed posterior) visible.

Description of BMNH I 8438. Mature male? Carapace not preserved. Sternum heart-shaped, slightly scalloped edges, ≥ 1.55 . Base of labium only visible. Right chelicera folded over left pedipalp coxa; left chelicera large hole into rock matrix, barely excavated; right chelicera with promarginal bifid tooth and more proximal tooth, retromarginal tooth row. Pedipalp coxae only bases preserved. Preserved coxae 0.97 long. Fe1 2.52, fe2 2.14, fe3 1.94, fe4 2.14. Opisthosoma ≥ 3.88 long, 3.50 wide. After removal of calcite, opisthosomal setae reveal positions of epigastric furrow and tracheal spiracle.

Remarks. Specimen IWCMS 1999.6 was mentioned by Jackson (1938). The locality was given (p. 69) as 'the Insect Bed in a shore exposure west of Gurnard Point, Thorness Bay'.

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