

MISSING LINKS BETWEEN ARGYRONETA AND CYBAEIDAE REVEALED BY FOSSIL SPIDERS

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ABSTRACT. *Argyroneta aquatica* (Clerck 1757) should be included in Cybaeidae Simon 1898. There is no justification for a monotypic family Argyronetidae; differences from other cybaeids are either specializations for aquatic life or derived with respect to other cybaeids. The features of a recently described Eocene spider, *Vectaraneus yulei* Selden 2001 are discussed, which place it together with *Argyroneta* in subfamily Argyronetinae Thorell 1870 of Cybaeidae. Fossil spiders intermediate between *Vectaraneus* and *Argyroneta* are reviewed.

Keywords: Argyronetidae, Argyronetinae, Desidae, Eocene, England, Isle of Wight

The European water spider, *Argyroneta aquatica* (Clerck 1757) is the only spider known to live for most of its life in fresh water. Most authors (e.g. Simon 1898; Platnick 1989, 1993, 1997; Bennett 1991; Grothendieck & Kraus 1994) agree that this species is close to Cybaeidae Simon 1898, but it has been placed in a monotypic family Argyronetidae by some (e.g. Roth 1967a; and references therein), thus emphasizing the unique adaptations for aquatic life which set this species well apart from its terrestrial relatives. In this paper I briefly review the morphological adaptations to aquatism in *Argyroneta* Latreille 1804; summarize the features of a recently described Eocene spider, *Vectaraneus yulei* Selden 2001, which place it in the cybaeid subfamily Argyronetinae, also recently emended by Selden (2001); and refer to other fossil spiders which are intermediate between *Vectaraneus* Selden 2001 and *Argyroneta*.

METHODS

Material studied.—*Elvina antiqua* (von Heyden 1859), holotype BMNH 58825, Natural History Museum, London, from Miocene Brown Coal of Grube Stöschen, near Linz am Rhein, Germany. *Vectaraneus yulei* Selden 2001, holotype BMBN 021960/1, Booth Museum of Natural History, Brighton, England; paratypes: IWCMS 1999.6, Isle of Wight Museum of Geology, Sandown, Isle of Wight, England; BMNH In 17151, BMNH I 8438, BMNH I 8440 and I 8452 (part and counterpart), Natural History Museum, London, Eng-

land; all from upper Eocene Bembridge Marls ('Insect Bed') of Gurnard Bay (except IWCMS 1999.6 which is from Thorness Bay), Isle of Wight, England. The following Recent material, all in the author's collection unless stated otherwise, was studied for comparative purposes. **Agelenidae:** *Agelena labyrinthica* (Clerck 1757), female, 19 July 1990, Innsbruck University, Austria, 11°20.5'E/47°15.6'N, rough ground; *Lycosoides coarctata* (Dufour 1831), female, May 1994, SW side of Soller harbor, Mallorca, garrigue; *Tegenaria silvestris* L. Koch 1872a, male, Black Ball, Dunster, Somerset, England, SS 982425, heathland near pines. **Anyphaenidae:** *Amaurobioides maritimus* O. P.-Cambridge 1883, female, Dunedin, New Zealand (coll. California Academy of Sciences); *Anyphaena accentuata* (Walckenaer 1802), female, 10 April 1996, Carnac, France (coll. D. Penney); *Hibana similis* (Banks 1929), female, 3 December 1995, El Valle, Panama (coll. D. Penney); **Cybaeidae:** *Argyroneta aquatica* Clerck 1757, female, 18 June 1981, Whixall Moss, Shropshire, England, SJ 49–36–; male, commercial slide, compressed mount (dated 1895); *Cybaeus hesper* Chamberlin & Ivie 1932, male, 30 October 1998, Redwood grove, Monte Rio, Sonoma County, California, 38°28.811'N/123°00.275'W; *Cybaeus patritus* Bishop & Crosby 1926, female, 15 July 1996, Highlands Biological Station, Macon County, North Carolina. **Dictynidae:** *Devade* Simon 1884 sp. female, 24 May 2000, bridge on Ghara-Aghatch river, Fars Province, Iran,

52°13'E/29°41'N; *Dictyna arundinacea* Linnaeus 1758; female, 23 May 1999, Manningtree, Essex, England, TM 081326, *Phragmites* marsh; *D. calcarata* Banks 1904, females, 30 June 1996, Wheeler Creek Nature Trail, Ventura County, California, riparian woodland; *D. innocens* O. P.-Cambridge 1872, female, 10 April 1995, Odeion, Paphos, Cyprus, 32°24'E/34°47'N; *D. reticulata* Gertsch & Ivie 1936, females, 30 June 1996, Rose Valley Lake, Ventura County California, on *Artemisia*; females, 25 August 1993, 5 mi. W of Middlegate, Nevada, 118°10'W/39°15'N, on *Artemisia*; *D. uncinata* Thorell 1856, female, 22 May 1999, Newbourne, Ipswich, Suffolk, England, TM 271435; *Lathys humilis* (Blackwall 1855), female, 22 May 1999, Newbourne, Ipswich, Suffolk, England, TM 271435; *Mallos pallidus* Banks 1904, female, 30 June 1996, Rose Valley Lake, Ventura County California, on *Artemisia*; *Tricholathys* cf. *spiralis* Chamberlin & Ivie 1935, females, 30 June 1996, Rose Valley Lake, Ventura County California, under stones in dry wash.

Material was studied using a Wild stereomicroscope; drawings were made with a *camera lucida* attachment; photographs were taken using a Minolta Dynax 9 camera attached to the microscope. All measurements are in mm. Abbreviations: 1, 2, 3, 4 = walking legs 1–4; AS = anterior spinneret; ch = chelicera; cx = coxa; lab = labium; MS = median spinneret; p = posterior; Pd = pedipalp; PS = posterior spinneret; st = sternum; tr = trochanter; tub = tubercle.

Argyroneta aquatica (Clerck 1757)

Remarks.—*Argyroneta aquatica* was first formally described and named by Clerck (1757:143–150; pl. 6, tab. 8, figs. 1, 2), in his genus *Araneus*, and the monotypic genus *Argyroneta* was erected for this species by Latreille (1804). Thorell (1870) created the subfamily Argyronetinae, which Menge (1871) elevated to family level in the following year. Simon (1898) recognized Argyroneteae as a tribe in Cybaeinae (Agelenidae), alongside Cybaeae and Desiae, and included the genera *Amphinecta* Simon 1898 and *Cambridgea* L. Koch 1872b in Argyroneteae. Family status for Argyronetidae was accepted by Dahl (1937), Kaston (1948), Petrunkevitch (1939) and Reimoser (1919). Kishida (1930) placed *Desis* and Cybaeinae in the family, and this

arrangement was followed by some other east Asian arachnologists, e.g. Komatsu (1961), Yaginuma (1955, 1958, 1960, 1962) and Paik & Namkung (1967). In his catalog, Bonnet (1955–9) included only the type genus, *Argyroneta*, in the family, whereas Roewer (1942–54) added *Gohia* Dalmas 1917 and *Urquhartia* Bryant 1933. Roth (1967a) both recognized and reviewed Argyronetidae, and the family status was used in the catalogs of Brignoli (1983) and Platnick (1989, 1993). However, Berland (1932), De Blauwe (1973), Gertsch (1949), Locket & Millidge (1953), Locket et al. (1974), Millot (1949) and Saito (1941) either ignored the family status or placed *Argyroneta* in Agelenidae, usually Cybaeinae (e.g. Grothendieck and Kraus 1994). Cybaeinae is commonly raised to family status in more recent works (e.g. Bennett 1991; Platnick 1993, 1997). Lehtinen (1967) limited Argyronetinae to the type genus but placed it and Cybaeinae in Dictynidae in his superfamily Amaurobioidea. Forster (1970) put Argyronetidae (also limited to *Argyroneta*) and Cybaeidae (elevated by him to family status) in Dictynoidea, but disagreed with most other authors on the close relationship between *Argyroneta* and Cybaeidae, preferring a closer alliance of *Argyroneta*, *Amaurobioidea* and Anyphaenidae. Platnick's (1997, 2001) latest catalogs put *Argyroneta* in Cybaeidae. Platnick (2001) pointed out that Argyronetidae Thorell 1870 actually has priority over Cybaeidae Banks 1892, but that the latter name is now in widespread use.

Numerous works have dealt with the aquatic mode of life and associated morphological and physiological adaptations of *A. aquatica*, especially Braun (1931, and references therein) and Crome (1953); and most works on spider respiratory physiology have studied the tracheal system of *Argyroneta*, e.g. Bertkau (1872), Bromhall (1987a), Lamy (1902) and Purcell (1910). There are a number of adaptations in *Argyroneta* for an aquatic life. A dense mat of fine setae covering the opisthosoma (Figs. 1, 2) acts as a plastron—an aquatic lung which allows air breathing under water, which works in the following way. The specialized setae (Braun 1931; Grothendieck & Kraus 1994: figs. 10–13) trap a bubble of air against the body surface and in connection with the tracheal spiracles. Oxygen diffuses from the surrounding water into the air bub-



Figures 1–2.—*Argyroneta aquatica* (Clerck 1757), adult male, microscope preparation. 1, whole body showing large chelicerae, heart-shaped sternum, long setae on base of posterior walking legs and sternum. 2, Opisthosoma showing dense felt of fine setae forming plastron, and long setae on base of posterior walking legs and sternum.

ble, which can then be exchanged in the spider's tracheal system in the normal way. Eventually, the concentrations of O_2 and CO_2 in the bubble decrease/increase respectively, so that the bubble needs to be replenished with fresh air. Long setae on the proximal podomeres of the walking legs (mainly 3 and 4) and the sternum (Figs. 1, 2) may aid in replenishing the air bubble and in carrying air to the bubble-nest. The tracheal spiracle in *Argyroneta* is rather wide and situated just posterior to the epigastric furrow. It leads to two large tracheae (Lamy 1902: fig. 56) which run forward into the prosoma before splitting into many finer tubes that extend into all parts of the prosoma, including the tarsi; similar tubules permeate the opisthosoma (Bromhall 1987a: figs. 2, 9–10), giving this spider the highest density of tracheae of any studied so far. In a study of the relationship between spider heart rates and locomotion (Bromhall 1987b), *Argyroneta* had the lowest heart rate of those studied. In general, spiders with low

heart rates have larger tracheal systems, and are either active or aquatic spiders. Presumably, gas exchange is faster when oxygen is delivered directly to tissues by the tracheal system than by intermediate transport in hemolymph. The fewer heart ostia of *Argyroneta* (Roth 1967a) might also be correlated with the diminished need for blood circulation. All of these features can be considered as adaptations for an aquatic mode of life.

Grothendieck & Kraus (1994) discussed aquatic adaptations and relationships of *Argyroneta*, and concluded that the adaptations of aquatic life were insufficient argument to separate the genus from other members of Cybaeinae (to which it is otherwise closely related, e.g. similarities in male copulatory organs), and *Argyroneta* is merely an aquatic specialized cybaeine(-id). These authors stated (Grothendieck & Kraus 1994: 272): 'Deshalb favorisieren wir die ursprüngliche Ansicht SIMONS (1898: 224, 230), wonach es sich bei *Argyroneta* um ein spezialisiertes Subtaxon

der Cybaeinae handelt. Es besteht keine Veranlassung, für die Wasserspinne eine separate Subfamilie Argyronetinae oder gar eine Familie Argyronetidae beizubehalten. Spezielle Lebensweise und Anpassungen (insbesondere Lage des Tracheenstigmas, relativ dichte Körper-Behaarung, Zahl und Anordnung der Bothriotrichen der Laufbein-Tarsen) stellen kein Argument zur Begründung einer solchen Rangstufe dar.' [Therefore we favor the original opinion of SIMON (1898: 224, 230), according to whom *Argyroneta* occupies a specialized subtaxon of the Cybaeinae. There is no reason to maintain a separate subfamily Argyronetinae or a family Argyronetidae for the water spider. The specialized way of life and adaptations (in particular the position of the tracheal stigmata, relatively thick body setation, number and arrangement of the trichobothria of the walking-leg tarsi) do not constitute an argument in favor of such a status.]

Vectaraneus yulei Selden 2001

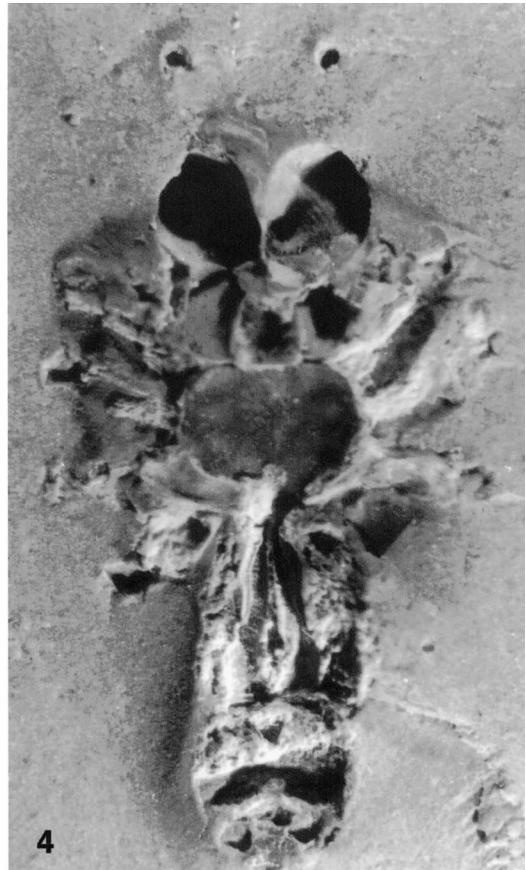
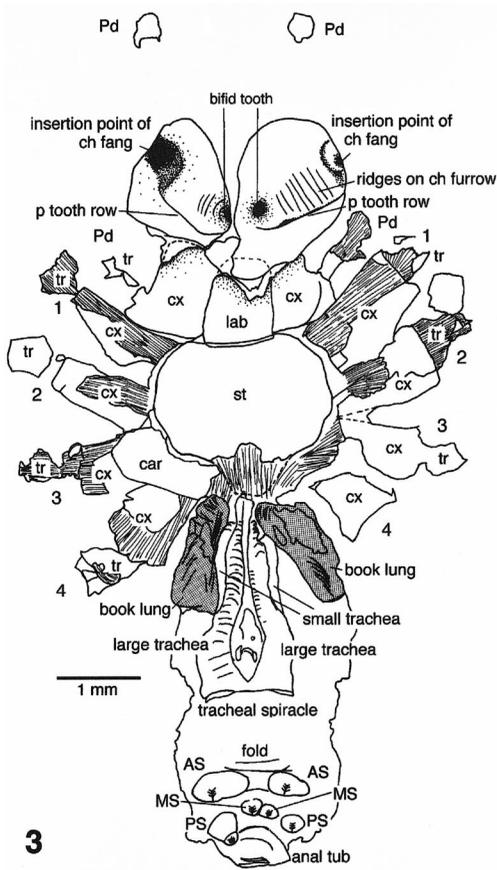
Vectaraneus yulei Selden 2001: 725–726, plates 1–5, text-figs. 1–9.

Remarks.—This taxon was erected for some fossil spiders from the so-called Insect Bed of the upper Eocene (c. 35 Ma) Bembridge Marls Member of the Bouldnor Formation (Solent Group) of Thorness Bay, Isle of Wight, England. The most remarkable aspect of the Bembridge spiders is the very fine preservation of internal anatomical structure by replacement with calcite (CaCO_3). Some organic matter is preserved, mainly cuticle lining the external mould cavities of the chelicerae and setae within the rock which can be seen when the specimens are observed under alcohol, but within the moulds of the chelicerae, labium and coxae, fine fibers of cream-colored calcite can be seen replacing muscle fibers, as described for the Bembridge Marls insects by McCobb et al. (1998). In the opisthosomae, book-lung lamellae are preserved in buff-colored calcite, and the book-lung atria anterior to the lamellae are lined with tiny, buff, drusy calcite crystals. The opisthosomae are filled with cream-colored calcite, which strikingly preserves the large tracheae running forward from a wide spiracle near the middle of the opisthosoma. The inner surfaces of these tubes bear spiral or scalariform reinforcements preserved in the same cream calcite. Spheroidal calcite filling the posterior

part of the opisthosoma of the holotype (presumably replacing silk glands or ova) was removed to reveal the spinnerets (Figs. 3, 4). Because of the preservation of internal anatomy, and their three-dimensional nature, the fossils must represent dead animals rather than molts. Detailed description of the species is given in Selden (2001) and a summary presented in Table 1, herein.

DISCUSSION

***Argyroneta* and cybaeid monophyly.**—Lehtinen (1967) was the first author to suggest the separation of Cybaeidae from Agelenidae. Following the realization that the presence of cribellum and calamistrum was plesiomorphic within Araneomorphae, he was able to place the ecribellate Cybaeinae and Argyronetinae in the ecribellate Dictynidae, based on similarity of genital organs, and separate from Agelenidae. Lehtinen defined Agelenidae on a combination of three characters: paired colulus, three tarsal claws, and lengthened posterior spinnerets. Forster (1970) and Forster & Wilton (1973) carried the separation of Agelenidae from Cybaeidae further or by placing Cybaeidae and Argyronetidae in Dictynoidea but Agelenidae in Amaurobioidea, primarily on tracheal system characters. Bennett (1991) reviewed the status of Cybaeidae to that date. He suggested that secondary pores on the vulva might be a useful taxonomic character, but found that they were rather widespread in Dictynoidea (*sensu* Forster 1970), and present both in cybaeids and *Argyroneta*. He discussed the status of cybaeids in relation to Agelenidae, concluding that cybaeids shared many of the characters of agelenids: ecribellate, three tarsal claws, single row of tarsal trichobothria, unnotched trochanters, and spinnerets not in a transverse row, but that these characters were either convergent or plesiomorphic at the family level. Characters separating cybaeids from agelenids: closely spaced anterior spinnerets, and narrowed posterior spinnerets with a very short distal segment, are widespread in other spiders. As pointed out by Griswold (1990:13) “The Agelenidae has performed for three-clawed ecribellate spiders much the same function as Amaurobiidae has for cribellates: a dumping ground for obscure and undistinguished forms. Not surprisingly, identification of a synapomorphy for the Agelenidae is difficult,



Figures 3–4.—*Vectaraneus yulei* Selden 2001, holotype part, female, BMBN 021960, upper Eocene, Bembridge Marls, Isle of Wight, England. 3, Camera lucida drawing, explanation for Fig. 4; 4, Specimen after excavation of fibrous calcite replacing fine tracheae (dashed line shows rear edge of sternum); spiniferets after removal of calcite spheroids.

but I think that Lehtinen (1967:401) has proposed just such a character. He stated that all true agelenids (including the genus *Agelena*) have a paired colulus consisting of two, more or less protruding, obtusely triangular plates. I have examined many genera of Agelenidae and found this character to be a conspicuous and consistent synapomorphy.” Cybaeids and *Argyroneta* (e.g. Roth 1967a; Grothendieck & Kraus 1994) lack a colulus, but do show paired setal patches. Roth (1967b) suggested using this character in conjunction with the length of the distal segment of the posterior spinneret in the separation of agelenines and cybaeines. Bennett (1991) concluded that Cybaeidae was monophyletic on the basis of shared possession of a suite of characters not found in the same combination elsewhere, and used male palp characters to demonstrate that

the outgroup of the cybaeids probably is, or lies within, Dictynidae.

Regardless of where cybaeids are placed, and their taxonomic rank, *Argyroneta* is recognized by nearly all authorities (e.g. De Blauwe 1973; Bennett 1991; Coddington & Levi 1991; Grothendieck & Kraus 1994) to be a derived cybaeid. The position of Cybaeidae is relevant to the position of *Argyroneta* because Argyronetidae is only sustainable if Cybaeidae is monophyletic without *Argyroneta*. Bennett (1991) was unable to find an autapomorphy for all species referred to Cybaeidae, though the presence of one or more peg setae on the patellar apophysis of the male palp serves as a character which distinguishes most species. The clade defined by this character excludes *Cybaeota*, for example, which lacks a patellar apophysis but was included in

Table 1.—Comparison of features of *Vectaraneus* Selden 2001 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	3 (1 + 1 bifid)	3–6	3	<i>toothed</i>
retromarginal teeth	2 + <i>carina/denticles</i>	5–9 minute	<i>denticles</i> [2 teeth]	<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	4123	1423	4123	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 & 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 [25]	13 [12]

Cybaeidae by Bennett (1988, 1991) because it could not be placed elsewhere. *Argyroneta* has a small patellar apophysis but lacks peg setae.

To summarize: Cybaeidae could be restrict-

ed to only those species which share the synapomorphy of peg setae on a patellar apophysis, which would leave at least *Cybaeota*, *Cybaeozyga* and *Argyroneta* as *incertae sedis*

within Dictynoidea, as Bennett (1991) concluded. The presently constituted Cybaeidae (e.g. Platnick 1997) encompasses these additional genera; thus the family lacks an autapomorphy but nevertheless can be defined on a suite of shared characters not found in the same combination elsewhere. Regarding *Argyroneta*, it has been pointed out by Grothendieck & Kraus (1994) that the differences between the genus and other cybaeids are almost entirely due to a secondary aquatic life. Thus, these character states are derived with respect to cybaeids, and to exclude *Argyroneta* from the Cybaeidae would render the family paraphyletic.

Looking at the differences between *Argyroneta* and *Cybaeus* in more detail [state in *Argyroneta* in brackets]. 1) setal fringe on the chelicera: present [absent]; since the setal fringe is absent in other aquatic spiders (e.g. *Desis*), it could be a hindrance in feeding and thus a derived characteristic due to aquatic life; moreover, its presence in potential outgroups (Agelenidae, Dictynidae) determines that its absence is derived. 2) a suite of characters related to the tracheal system (see Table 1), e.g. large tracheal trunks, extensive tracheation, broad spiracle, etc., are clearly related to an aquatic mode of life, and therefore derived. 3) extensive, fine setation of the abdomen (plastron) and long setae on proximal podomeres of posterior legs in *Argyroneta* are clearly derived features related to air uptake from the water surface. 4) heart ostia three pairs [two pairs] (Roth 1967a, Table 1); this reduction of heart ostia could be related to the reduced need for blood circulation because of the better tracheal penetration (cf. lower heart rate recorded for *Argyroneta* by Bromhall 1987b). 5) tarsal trichobothria in a single row [double row]; because a single row of tarsal trichobothria occurs in putative sister groups to Cybaeidae (Agelenidae and Dictynidae), a double row must be considered derived.

To conclude this discussion, Cybaeidae would be paraphyletic without *Argyroneta*; recognition of Argyronetidae with the same rank as Cybaeidae is unsustainable, but subfamily Argyronetinae could be justified. The large number of derived characters separating *Argyroneta* from other cybaeids predicts the existence of intermediate taxa.

***Vectaraneus*.**—Of all the features of *Vectaraneus*, the wide tracheal spiracle, situated

half-way between the epigastric furrow and the base of the spinnerets, with large tracheae running forwards into the prosoma, are the most characteristic. 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. *Vectaraneus* is in this group of families, excluding Hahniidae because of their transverse spinnerets. Table 1 compares morphological features of *Vectaraneus*, Anyphaenidae, Cybaeidae (including *Argyroneta*), and Desidae (including *Desis*). It can be seen that *Vectaraneus* shares more character states with Cybaeidae (27/33) than with any other (see Selden 2001 for detailed discussion). It is possible that *Vectaraneus* represents another parallel development of aquatic life in a different group of spiders, but this hypothesis requires the unsubstantiated assumption of more convergence, and nearly all other characters are consistent with *Vectaraneus* being a cybaeid. As discussed above, the monophyly of Cybaeidae is not based on synapomorphies but on a unique combination of characters; *Vectaraneus* shares these characters, where they are preserved.

As discussed above, Grothendieck & Kraus (1994) considered *Argyroneta* to be a cybaeid which shows adaptations for aquatic life, including a wide, forwardly positioned, tracheal spiracle, large tracheal trunks running into prosoma and extensive tracheal system. *Vectaraneus* shows these features also, but differs in that the spiracle is situated half-way between the epigastric furrow and the spinnerets. However, the spiracle occurs in this position in juvenile *Argyroneta* (Crome 1953: figs 51–54). *Vectaraneus* also lacks the plastron. Therefore, *Vectaraneus* most closely resembles juvenile *Argyroneta*. If *Argyroneta* is a cybaeid which has become adapted to an aquatic existence, then *Vectaraneus* may be considered to occupy a part-way stage in this trend. Juvenile *Argyroneta* show a stage in the development of aquatic adaptations seen in the adult stage of *Vectaraneus*.

Other fossils referred to *Argyroneta*.—

Von Heyden (1859) described a fossil spider from the Miocene Brown Coal of Grube Stöschchen, near Linz am Rheine, Germany, as *Argyroneta antiqua* von Heyden 1859, placing it in that genus on account of its general appearance and its preservation in a swampy palaeoenvironment, 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* Heer 1865. In regard to this specimen, Heywood (footnote in Heer 1876: 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* [sic.]; 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* [sic.], 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: 224) suggested that *Argyroneta antiqua* von Heyden 1859 probably belonged in Tubitelariae (a name no longer in use for 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. Re-study of the holotype of *Argyroneta antiqua* von Heyden 1859 by Selden (2001) concluded it is *Araeomorpha incertae sedis*, but not an *Argyroneta*, and it was referred to *Elvina* Thorell 1870. As for *A. longipes* Heer 1865, Thorell (1870) was certain that it did not belong in *Argyroneta*, and I concur.

Bertkau (1878) described a collection of fossil spiders and a millipede from the Brown Coal of Rott, including 19 specimens he referred to *Argyroneta antiqua*; ten (including von Heyden’s holotype) from the Kieselschie-



Figure 5.—*Argyroneta* sp. BMNH In 39930, Miocene Brown Coal of Rott, Germany; see Bertkau (1878).

fer (‘flint-slate’) and nine from the Blätterkohle (‘leaf-coal’). These are now distributed in a number of museums, including The Natural History Museum, London (BMNH 59627 and BMNH In 39930 (Fig. 5)), American Museum of Natural History (AMNH 26275) and the George Statz Collection in the Los Angeles County Museum of Natural History (including LACM 3086, figured by Furst 1959, 1970). Bertkau gave a detailed description of the species, including the heart-shaped sternum, and discussed the nature of prominent parallel bands (‘Längstreiffen’) on the opisthosomae of the Kieselschiefer specimens, concluding that these represented a prominent tracheal system. He suggested that the new specimens were conspecific with the holotype of *A. antiqua*, 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. Bertkau was familiar with *Argyroneta*, and with spider tracheal systems in general, having published on spider respiratory organs a few years earlier (Bertkau 1872). Thus, Bertkau (1878: 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.” [Certainty of this question would, however, be of great

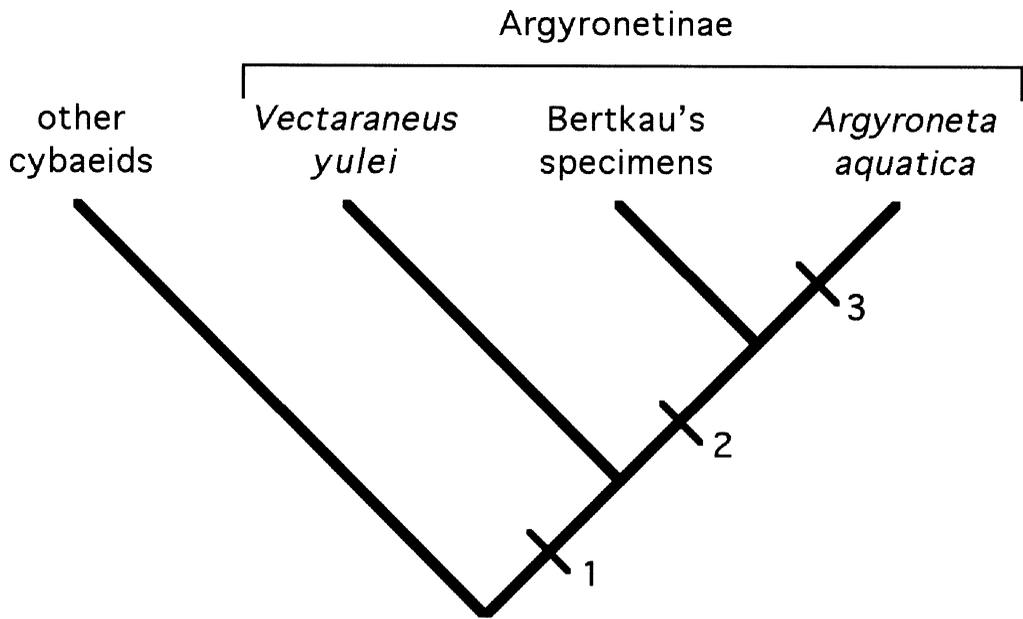


Figure 6.—Cladogram showing hypothesized relationship between *Vectaraneus yulei*, *Argyroneta aquatica*, Bertkau's specimens, and other Cybaeidae. Characters at node 1 defining Argyronetinae: enlarged tracheal trunks running into prosoma, and wide tracheal spiracle situated well forward of base of spinnerets; 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.

interest, since it seems to me to be a particularly instructive case of the Theory of Evolution.]

In his study of AMNH 26275, Petrunkevitch (1946) showed that this specimen was not conspecific with the holotype of *Argyroneta antiqua*, and neither are the BMNH specimens 59627 and In 39930 (Selden 2001). Bertkau's specimens are, however, close to the extant *A. aquatica*, differing, as Bertkau (1878) mentioned, by the more posterior position of the tracheal spiracle. In this, they resemble *Vectaraneus*. However, *Vectaraneus* lacks 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. Thus, the Bertkau specimens, which all appear to be conspecific, sit between *Vectaraneus* and modern *Argyroneta*. It is likely that they could be included in the modern genus because they share the same characters except for the more posterior position of the tracheal spiracle. No taxonomic changes are suggested here while Ph.D. research is being conducted on these specimens in Manchester by Richard Cutts. Figure 6

summarizes the phylogenetic hypothesis. Selden (2001) emended Argyronetinae as follows: "Cybaeidae with enlarged tracheal trunks running into prosoma; wide tracheal spiracle situated well forward of base of spinnerets."; included genera *Argyroneta* and *Vectaraneus*.

Mode of life.—The rock matrix preserving *Vectaraneus* is a massive, fine limestone which resembles the lithology of the main, tabular, insect-bearing horizon occurring near the base of the Bembridge Marls (Jarzembowski 1980; McCobb et al. 1998). Biota associated with the spiders include the reed *Typha*, the crustacean *Branchipodites vectensis*, Hymenoptera, Diptera, and juvenile Araneae. The arthropods are commonly in distinct horizons which suggests mass mortality, e.g. following a synchronous emergence, or aggregations accumulated by water surface tension or adhesion to floating vegetation. 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; Collin-

son 1983, 1990; Collinson et al. 1993), perhaps similar to the Florida Everglades today. This evidence points to *Vectaraneus yulei* as living in a marshy habitat, and its morphological adaptations suggest it was possibly amphibious in its mode of life.

ACKNOWLEDGMENTS

I thank Ed Jarzembowski (Maidstone Museum, Kent) for kindly passing BMBN 021960/1 on for study; John Dalingwater (Hale, Cheshire) for help with scanning electron microscopy; Martín Ramírez (Universidad de Buenos Aires) for helpful discussion on spider tracheal systems; Derek Siveter (University Museum, Oxford) for comments on taxonomy; Yuri Marusik (University of Magadan, Russia), David Penney (Manchester University) and Charles Griswold (California Academy of Sciences) for provision of comparative material; Lindsey Groves (Los Angeles County Museum of Natural History) for drawing my attention to the George Stutz Collection; Andrew Ross (The Natural History Museum, London), Stephen Hutt (Museum of Geology, Isle of Wight, England), and John Cooper (Booth Museum of Natural History, Brighton, England) for help with literature and the loan of fossil specimens in their care; and Margaret Collinson (University of London) for discussion on the palaeoecology of the Bembridge Marls. I thank two anonymous reviewers for useful comments.

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Manuscript received 1 July 2001, revised 6 February 2002.