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Autapomorphies of the Endophragmal System in Trichodactylid Freshwater Crabs (Crustacea: Decapoda: Eubrachyura)

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ABSTRACT An examination of the thoracic endophragmal system in trichodactylid freshwater crabs revealed several derived features that appear restricted to this family. Trichodactylids have a highly reduced sella turcica with a rim-like overall configuration; as a consequence of sella turcica reduction the median septum is dorsoventrally diminished and exposed along its length. In addition, interosternite 7/8 is medially erased with the remnants restricted to the lateral regions of the sternum. The configurations of the sella turcica and interosternite 7/8 in trichodactylids underscore the monophyly of this family. The Dilocarcininae is characterized by having interosternites 5/6 through 7/8 restricted to the lateral sectors of the sternum, the lateral remnants of interosternite 4/5 forming prominent, rib-like ridges oriented diagonally to the longitudinal axis of the crab, and the median septum forming with interosternite 4/5 a Y-shaped pattern. These autapomorphies of the endophragmal system separate the trichodactylids from all other eubrachyurans and emphasize the morphological distinctness of the group. A description of the trichodactylid endophragmal junction plate is also provided. *J. Morphol.* 256:23–28, 2003.

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The Trichodactylidae is a freshwater crab family found primarily in the drainage basins of the rivers Amazon, Orinoco, and Paraguay-Paraná in South America, with a small number of taxa distributed in Mexico and Trinidad. A number of authors (Ortmann, 1897; Rathbun, 1904, 1905, 1906; Alcock, 1910; Bouvier, 1917a,b, 1921; Colosi, 1920; Bott, 1955; Balss, 1957) assumed that the freshwater crabs form a monophyletic group and placed all of the world's freshwater crabs in a single family, the Potamonidae. Although each of these authors proposed a different classification for the group, all recognized the distinctiveness of the trichodactylids (which lack spines on the dactyli of the walking legs and have a slim third maxilliped merus) by placing them in their own subfamily, the Trichodactylinae. Recent taxonomies (Bott, 1970; Bowman and Abele, 1982; Rodríguez, 1992; Magalhães and Türkay,

1996a,b,c) continue to recognize the Trichodactylidae as a unique family of freshwater crabs. Indeed, the monophyletic status of the Trichodactylidae has never been seriously questioned because these crabs possess a distinct groundpattern among the freshwater crabs in particular, and within the Eubrachyura in general. The Trichodactylidae has been the subject of several recent taxonomic revisions (Rodríguez, 1992; Magalhães and Türkay, 1996a,b,c) which recognized two subfamilies (Dilocarcininae and Trichodactylinae), 16 genera, and 49 species and subspecies and this has been accepted by most authors.

The cladistic relationships of genera within the two trichodactylid subfamilies have recently been debated (Morrone and Lopretto, 1996; Sternberg, 1997). However, the cladistic studies aim at assessing the relationships within the Dilocarcininae and Trichodactylinae (Rodríguez, 1992; Morrone and Lopretto, 1996; Sternberg, 1997) have been hampered by the unclear taxonomic position of the Trichodactylidae within the Eubrachyura. The uncertainty concerning the choice of suitable outgroup taxa for the Trichodactylidae has made it difficult to assign character state polarities necessary for the determination of hierarchical relationships within this family.

The Trichodactylidae has been thought by some workers (Rodríguez, 1986; Ng and Rodríguez, 1995) to be related to the African potamonautid genus *Erimetopus*, but their judgment was based primarily on superficially similar (but often convergent) characters of the carapace. In addition, trichodactylids have been considered (Guinot et al., 1997) to be allied to the Old World Potamoidea as members of

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the Potamidae. Guinot et al. (1997) stated that it is "...questionable whether the Palaeotropical family Potamidae is phylogenetically distinct from the Neotropical Trichodactylidae; in both of them plesiomorphy is apparent in the mouth parts, in the very simple first pleopod, and the long pleopod 2." However, it is also questionable to group families on the basis of generalized characters such as these and it is clear that this hypothesis of relationship owes a great deal to previous schemes of freshwater crab taxonomy which placed all existing families (including the Trichodactylidae) as subfamilies of the Potamidae (Ortmann, 1897; Rathbun, 1904, 1905, 1906; Alcock, 1910; Bouvier, 1917a,b, 1921; Colosi, 1920; Bott, 1955; Balss, 1957).

Ortmann (1902: 312), on the other hand, discounted any close relationship between trichodactylids and the remaining true freshwater crab groups, noting that, between trichodactylids and other freshwater crabs: "...transitional forms to any of the other subfamilies [of freshwater crabs] are not known, and the *Trichodactylinae* [=Trichodactylidae] are morphologically isolated and sharply defined...the *Trichodactylinae* form a group that is much more sharply isolated, systematically, and that has little to do with the family *Potamonidae* [=Potamoidea]." It should be noted that transitional forms linking the trichodactylids with other New or Old World freshwater crabs have not been forthcoming since Ortmann's time, so his observations that the Trichodactylidae are morphologically isolated and sharply defined still stands.

Traditional freshwater crab classifications (Bowman and Abele, 1982) imply a trichodactylid-potamid sister-group hypothesis, but this has been challenged by Rodríguez (1992) who proposed that members of the Carcininae were the most plausible sister-group of the trichodactylids, based on a shared overall morphology. This hypothesis clearly broke with tradition and was tested by Sternberg (1998) and Sternberg et al. (1999), who found evidence supporting the placement of the trichodactylids within the Portunoidea. It should also be noted that no apomorphies were identified by the former authors that would tie the trichodactylids to either the New World Pseudothelphusoidea or to any Palaeotropical freshwater crab family. Furthermore, trichodactylids share apomorphies with several portunoid genera and with a number of geryonid genera that were placed by Manning and Holthuis (1981) in the Portunoidea. These apomorphies include a broadly triangular male abdomen with segments a3-a5 often fused, a carapace lateral margin that is well-defined, a posterior carapace carina that is sharp and pronounced, a distinct "portunoid lobe" on the maxilliped 1 endopod, and a geryonid/carcinine-like male first pleopod (Sternberg, 1998). It is of interest to note that the same apomorphies are shared by some cancrids and by the Pirimelidae. The shape of the trichodactylid third

maxilliped is strikingly similar to that of the carcinine genus *Nectocarcinus*. Further, the fifth pereopod of dilocarcinines is lined with fine setae (like *Carcinus*) and the dactylus is lanceolate (also like *Carcinus*). The sternum of the Dilocarcininae is also topographically equivalent to that seen in many geryonids and portunoids. Thus, a number of modified character complexes suggest that a portunoid subclade may be the sister taxon of the Trichodactylidae.

However, the carapace morphology of the trichodactylines is strikingly unlike that of either geryonids or portunoids. The fifth pereopod of the Trichodactylinae is in addition styliiform, not lanceolate, as in dilocarcinines. However, some portunoids such as *Catoptrus* and *Libystes* also have somewhat similar styliiform fifth pereopod dactyli, as do all geryonids. The carapace morphotype of trichodactylines is reminiscent of varunid grapsoids and thus is strikingly unlike the more carcinine-like carapace outlines seen in the Dilocarcininae. Finally, among the many disparate genera of the Trichodactylidae, only the dilocarcinines possess fifth pereopods, a male abdomen, and sternum that are distinctly portunoid-like. These observations pose a problem for cladistic resolution of genera within the family, because of the uncertainty in determining whether the dilocarcinines or trichodactylines have the more basal groundpattern that is reflective of sister-group relationships. We therefore think, in light of the above, that the unequivocal assignment of the Trichodactylidae to the Portunoidea will depend on the identification of a trenchant, congruent synapomorphy common to both groups.

Endophragmal System

The present work describes specifics of the sella turcica (or "Turk's saddle") and junction plate (see Secretan, 1998) of the trichodactylid endophragmal system for the first time in an attempt to identify new characters that might clarify the systematic position of this family. Magalhães and Türkay (1996a) investigated the endophragmal system in their revision of trichodactylid generic groupings, although they focused more on general organizational patterns as opposed to individual components. The endophragmal system of the Trichodactylidae exhibits a highly derived level of interruption of the medial region of the interosternite partitions, wherein sternal phragmae (interosternites) 4/5 through 7/8 are limited to the lateral regions of the sternum. Note that from the ventral perspective the interosternal phragmae appear as sutures that extend variably across the sternum. Magalhães and Türkay (1996a) found that patterns of interosternite interruption are diagnostic for the Trichodactylinae and Dilocarcininae and for the dilocarcinine tribes Dilocarcinini and Valdiviini. A similar pattern of sternal phragmae interruption is also seen in sev-

eral portunoid groups (e.g., some members of the Polybiinae and many taxa in the Portuninae; Guinot, 1979). However, putatively basal portunoids like *Carcinus* and the geryonids have a complete interosternite 7/8 and this observation raises doubts as to the homology of the portunoid and trichodactylid sternal patterns. It is likewise relevant to note that carcinoplacine goneplacids, some bythograeids, and genera in the incertae sedis "subfamily" Troglolacinae have sternite patterns close in organization to those of trichodactylids.

In order to determine whether the trichodactylid endophragmal organization is related to that seen in portunoids, the internal aspects of trichodactylid medial interosternite interruption were analyzed and compared with published descriptions of portunoid sternal patterns (Cochran, 1935; Guinot, 1979).

Sella Turcica and Junction Plate

The sella turcica is a prominent feature of the endophragmal system of eubrachyuran crabs that has been used as a defining character of the Eubrachyura (Guinot, 1979; Secretan, 1998). In most representatives of the Eubrachyura the sella turcica is a prominent and well-defined anatomical unit (see plates in Guinot, 1979; also Secretan, 1998). Although the sella turcica is a complete, paired intertagmal phragma that is medially contiguous, the posterior sheet is part of the abdominal tagma, whereas the anterior region emerges from the eighth sternite. The conformation of this unit in *Cancer borealis* (Fig. 1A) is typical for the Eubrachyura. The moderately elongated sella turcica of *Cancer*, covering a large portion of the median septum (Guinot, 1979) in dorsal view, is typical of that seen in nearly all heterotreme and thoracotreme superfamilies (see Guinot, 1979) and appears to be part of the eubrachyuran groundpattern.

The junction plate unites the endopleurites and the interosternites and this unit arises from the fusion of these two regions of the endophragmal system. The junction plate of trichodactylids has not been previously described, we do so herein.

MATERIALS AND METHODS

Three approaches for examining the trichodactylid sella turcica and junction plate were used. First, specimens of *Poppiana dentata* (Randall, 1839) were collected from ponds and ditches near Guanare, Venezuela, and then killed by refrigeration. Freshly dead specimens were maintained at ambient temperature for 1–2 days to allow enzymes released from the viscera to digest the musculature and to prevent damage to interosternites. Following removal of the carapace the endophragmal system was gently rinsed with warm water to remove decayed tissues and the skeleton was then placed in 70% ethanol to avoid desiccation, as that would shrivel the phragmae. (The endophragmal systems of the trichodactylid taxa examined are weakly calcified.) Second, specimens of *Trichodactylus* Latreille, 1828, already preserved in 70% ethanol, were transferred to a dish containing various liquid

dishwashing detergents and were then incubated at 55°C for 2 days. This softened the tissue so that viscera and muscle fibers could be carefully removed using fine forceps and a dissecting microscope. Third, museum specimens (from the National Museum of Natural History, Smithsonian Institution; abbreviated USNM) were examined by gently opening up the carapace followed by removing the viscera with forceps so that the phragmae of interest were exposed.

RESULTS

The conformation of the sella turcica of the trichodactylid endophragmal system was found to be unique to the family (Fig. 1B,C). First, the sella turcica is greatly shortened (Fig. 1B,C), in contrast to the states observed in other eubrachyuran taxa (Cochran, 1935; Guinot, 1979; Secretan, 1998) where this phragma covers the dorsomedian region of the eighth sternite. The shortening of the sella turcica exposes the median septum along the entirety of its length (Fig. 1C) and the posteromedial region of the structure is seen to arise from sternite 8 (Fig. 1D). Second (undoubtedly a consequence of shortening of the unit), the shape of the sella turcica is rim-like, a condition that appears to be unique to the Trichodactylidae (Fig. 1B,C,E). Representatives of the Dilocarcininae (*Poppiana dentata*) (Fig. 1B,D) and Trichodactylinae (*Trichodactylus* sp.) (Fig. 1C) both have a shortened sella turcica that is independent of sternal width, patterns of endosternite medial interruption, and gender. Partial dissections of other trichodactylids (*Dilocarcinus pagei*, USNM 19531, and *Sylviocarcinus devillei*, USNM 231583) revealed that a reduced, rim-like sella turcica is autapomorphic for this family and thus has high utility as a family-level diagnostic character. The rim-like sella turcica was not discussed by Magalhães and Türkay (1996a), although careful study of their autoradiograph photos (e.g., fig. 40) does show species with a sella turcica whose structure is consistent with those presented here.

In association with the reduced sella turcica, the median septum was found to be diminished in relief, that is, to have a conformation of a low and thick ridge, in all the trichodactylid species examined (Fig. 1B,C,E). In the Trichodactylinae the median septum extends to the median termini of the interrupted interosternite 6/7 (Fig. 1C). Dilocarcinines, on the other hand, have the median septum extending to the median termini of interosternite 4/5; in dorsal view, the median septum and interosternite 4/5 forms a Y-shaped pattern (Fig. 1B). The Y-shaped pattern is in part a consequence of the orientation of interosternites 4/5 (see below).

Magalhães and Türkay (1996a) described the sternal patterns of the trichodactylid subfamilies and the two tribes contained within the Dilocarcininae. The Dilocarcinini, Trichodactylinae, and Valdivini all have interosternite 7/8 restricted to the lateral region of the sternum; indeed, interosternite 7/8 is so reduced that it is hard to detect in dorsal view

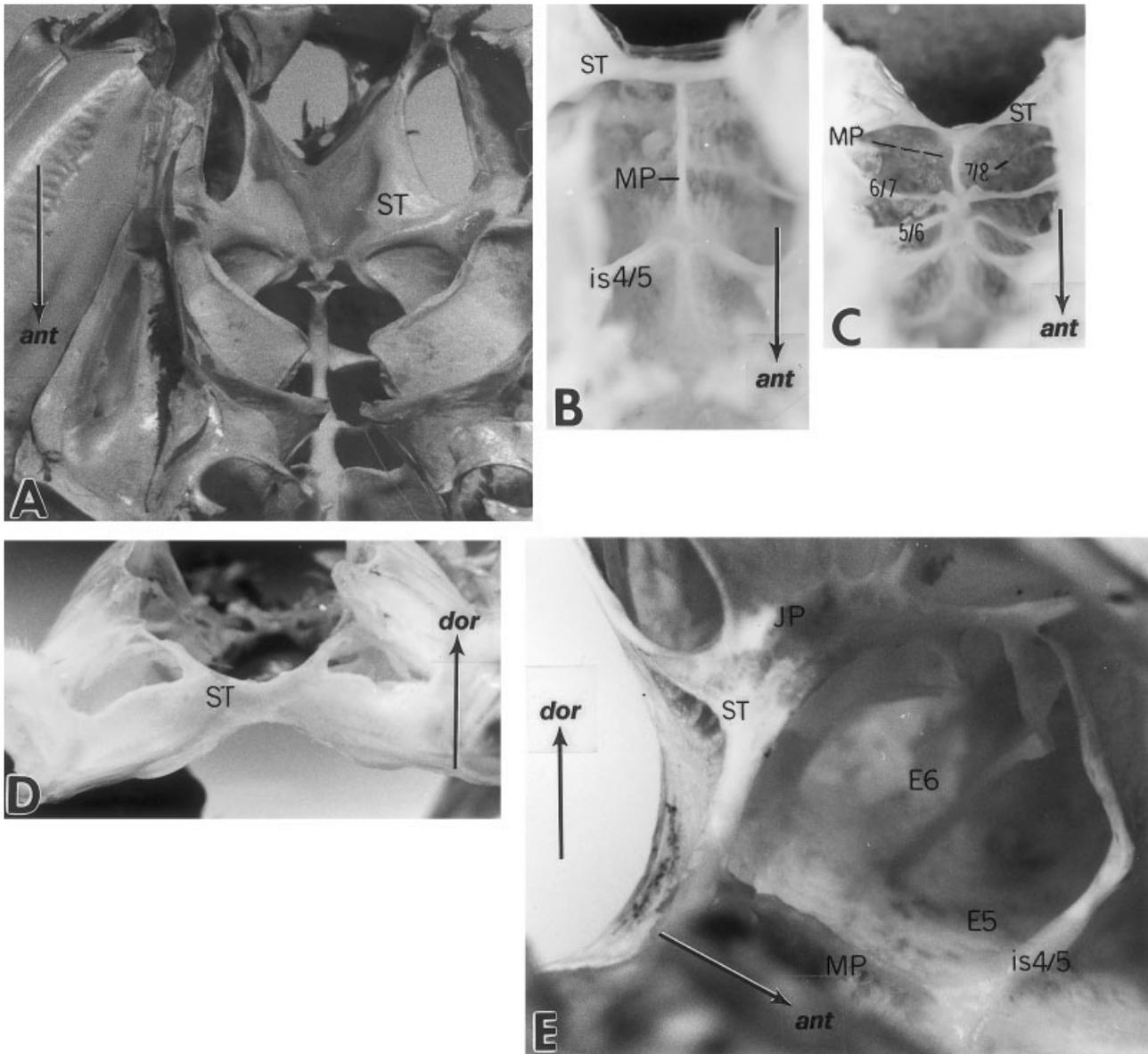


Fig. 1. Organization of the sella turcica in *Cancer*, a generalized eubrachyuran, and representatives of the trichodactylid subfamilies Dilocarcininae and Trichodactylinae. **A**: Dorsofrontal view of the sella turcica in the *Cancer borealis* endophragmal system. **B**: Dorsal view of the sella turcica and median region of the interosternites in the *Poppiana dentata* endophragmal system. **C**: Dorsal view of the sella turcica and median region of the interosternites in the endophragmal system in *Trichodactylus* sp. **D**: Posterior view of the sella turcica in *Poppiana dentata*. **E**: Lateral region of the sella turcica in *Poppiana dentata*. E5 and E6, sternites 5 and 6, respectively; 5/6, 6/7, and 7/8, interosternites 5/6, 6/7, and 7/8; is4/5, interosternite 4/5; JP, junction plate; MP, median partition (septum); ST, sella turcica; *ant*, anterior; *dor* dorsal.

(Fig. 1B,C). Inasmuch as the laterally restricted state of interosternite 7/8 is consistently present throughout the Trichodactylidae, in addition to being apomorphic, this character along with the reduced sella turcica and median septum can be considered diagnostic of the family.

The relationship of interosternites 4/5 through 6/7 constitutes an autapomorphy of the Dilocarcininae. The medial termini of interosternite 4/5 are juxtaposed and nearly complete, whereas interosternites 5/6 and 6/7 have the median region erased (Fig. 1B,E; see Magalhães and Türkay, 1996a). In addition,

another defining character of this subfamily is the diagonal orientation of the rib-like interosternite 4/5 relative to the longitudinal axis of the crab (Fig. 1B,E). As can be clearly seen in *Poppiana dentata* (Fig. 1B), the medial termini of interosternite 4/5 are confluent with the anterior end of the median septum to form the Y-shaped pattern discussed above.

The pattern of interosternites 4/5 through 6/7 in the Trichodactylinae (Fig. 1C) is consistent with that observed in geryonids and basal portunoids.

Figure 2A depicts the junction plate of *Trichodactylus fluviatilis*, USNM 71266, from the medial per-

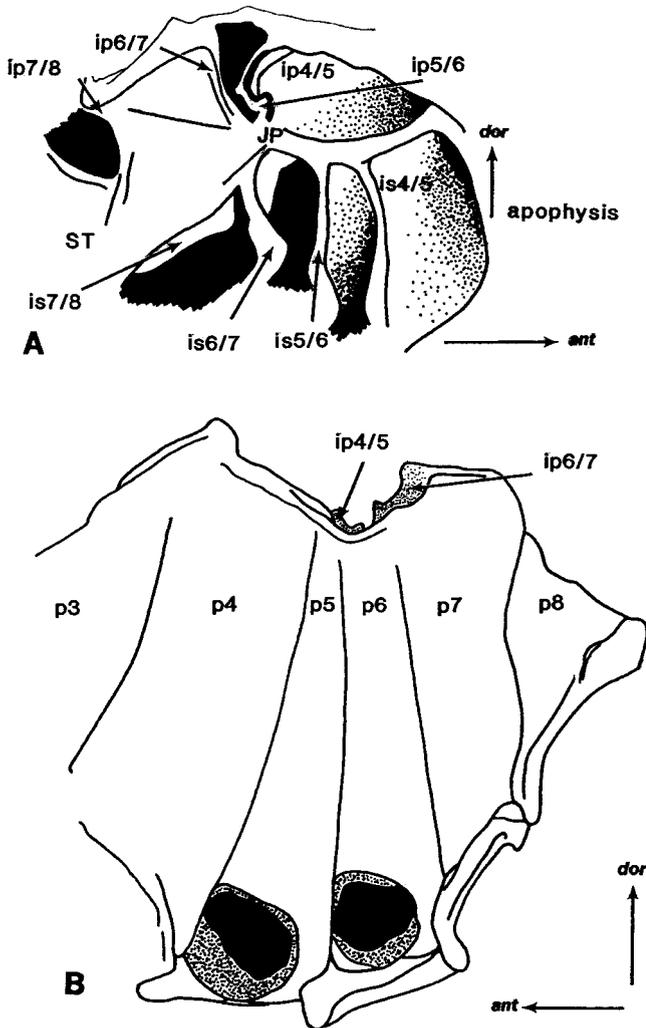


Fig. 2. Organization of the junction plate and posterior pleural roof in *Trichodactylus fluviatilis*. **A**: medial view of the junction plate (JP), interosternites (is4/5 to is7/8), interpleurites (ip4/5 to ip7/8), apophysis, and sell turcica (ST). **B**: Dorsolateral view of the roof of pleurites (p) 3–8 and exposed interpleurites ip4/5 and ip6/7. *ant*, anterior; *dor*, dorsal.

spective; Figure 2B shows the pleural roof of the same specimen. The conformation of the junction plate (and pleural roof) was found to be nearly identical in *T. fluviatilis*, *Dilocarcinus pagei*, and *Sylviocarcinus devillei*. Several aspects of the interpleurites distinguish trichodactylids from *Carcinus* (see Secretan, 1998). First, interpleurites 4/5, 5/6, and 6/7 in trichodactylids are medially juxtaposed with interosternite 5/6 barely visible medially and dorsally (Fig. 2A,B). Second, in medial view the medial margins of interosternites 4/5 and 6/7 have a distinctly sigmoidal outline (Fig. 2A). And third, the pleurite 7 cavity is medially expanded, as long as that of pleurite 4 (Fig. 2B). Given that too little is known about the junction plate of other eu-brachyurans, this description is provided so that future comparisons can be made.

CONCLUSION

The Trichodactylidae undoubtedly forms a natural group based on the greatly shortened, rim-like sella turcica, the dorsoventrally reduced median septum, and on the extensive medial interruption of interosternite 7/8. Similarly, the Dilocarcininae is monophyletic based on characters of interosternite 4/5, which has a prominent rib-like structure with a diagonal orientation in dorsal view and is medially continuous with the anterior region of the median septum to produce a Y-shaped pattern. In addition, interosternites 5/6 through 7/8 are restricted to the lateral regions of the sternum (Fig. 1B,E). In contrast to these results, the endophragmal skeleton of all Old World freshwater crabs examined, and representatives of the New World Pseudothelphusidae, all have a well-developed sella turcica of normal length, a distinct median septum, and interosternite 7/8 is not medially erased (Sternberg and Cumberland, in prep.) as do geryonids, many portunoids, and xanthoids (see Cochran, 1935; Guinot, 1979).

The trichodactylid endophragmal system can be clearly distinguished from the geryonid pattern of organization (Guinot, 1979). Most character states of the trichodactylid endophragmal system clearly separate this clade from portunoids. A number of portunoids have the sella turcica greatly lengthened as well as a prominent median septum that extends to sternites 1/2 (Cochran, 1935). The extended sella turcica/median septum in portunoids like *Callinectes sapidus* is related to the exaggerated development of the fifth pereopod a-branch of the musculus promotor; this muscle branch is attached anteriorly to the median septum and thus extends forward to sternite 5 (Cochran, 1935). Noting, however, that portunoids such as *Carcinus* do not exhibit an overdevelopment of the fifth pereopod musculus promotor a, the apomorphies observed in portunoids like *C. sapidus* appear to be diagnostic for a derived subclade. The characters of the endophragmal system of the Trichodactylidae thus do not falsify the placement of this family in the Portunoidea s.l.

It should also be noted that medial reduction of interosternite 7/8 was described by Cochran (1935) for *Callinectes sapidus*, although the extent this interosternite is reduced in *Callinectes* is not as great as that seen in the trichodactylids. A number of other swimming portunoids also reveal varying degrees of interosternite 7/8 medial reduction. Yet again, other portunid genera (e.g., *Carcinus* and *Coenophthalmus*) lack the medial reduction of interosternite 7/8. These observations then raise the question of whether interosternite 7/8 interruption emerged in parallel in the Trichodactylidae and portunid subclades or whether this apomorphy is an indicator of deeper affinities (e.g., trichodactylids as an aberrant but derived portunid clade).

One trenchant conclusion is that the trichodactylid endophragmal organization is phenetically far removed from that of other eubrachyurans.

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