

Homologies of the carpal bones in flying squirrels (*Pteromyinae*): a review

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Abstract. The homologies of the carpal bones of flying squirrels, presented by Oshida et al. (2000a, b), are reviewed, together with the evidence supporting traditional homology assessments. Evidence for the homology of the styliiform cartilage of flying squirrels with the hypothenar cartilage of other squirrels is also reviewed. Development, articulations, topography, and muscle insertions favor both the traditional hypothesis of homology assessments of the carpal bones and also the hypothesis that the styliiform cartilage is homologous with the hypothenar cartilage.

Key words: carpal homologies, flying squirrels, *Pteromyinae*, styliiform cartilage.

In two papers, Oshida et al. (2000a, b) described the styliiform cartilage of flying squirrels and suggested that it is homologous with the pisiform bone of other mammals. This is a revolutionary interpretation of the homology of the carpus. It contrasts with the hypothesis of Thorington et al. (1998) that the styliiform cartilage of flying squirrels is homologous with the hypothenar cartilage of other squirrels. In addition, the homology assessments of Oshida et al. (2000a, b) for all the proximal carpal bones differ fundamentally from the more traditional hypothesis followed by many authors, e.g. Hill (1937), Bryant (1945), Holmgren (1952), Grassé and Dekeyser (1955), Thorington (1984), Thorington et al. (1997), and Stafford and Thorington (1998). If true, the Oshida et al. hypothesis illustrates the most radical rearrangement of the carpal bones in mammals. We list the differences in the homologies between the traditional and the Oshida hypotheses (Fig. 1).

1. The scaphoid bone of Oshida et al. (2000a, b) is considered by other authors, cited above, to be a scapholunate bone, the combined scaphoid and lunate bones.
2. The lunate bone of Oshida et al. (2000a, b) is considered by other authors to be the triquetral bone.
3. The triquetral bone of Oshida et al. (2000a, b) is considered by other authors to be the pisiform bone.
4. The styliiform cartilage is considered by Oshida et al. (2000a, b) to be derived from

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the pisiform bone. Gupta (1966) suggested that it is derived from an accessory carpal (i.e. the ulnar sesamoid) found in some other mammals. Thorington et al. (1998) and Thorington and Darrow (2000) considered it homologous to the hypothenar cartilage of other squirrels. Most other authors have not considered the homology of the styliiform cartilage.

5. A muscle inserting on the styliiform cartilage is identified by Oshida et al. (2000a, b) as an accessory insertion of *M. flexor carpi ulnaris* in agreement with Gupta (1966) and Johnson-Murray (1977). Thorington et al. (1997, 1998), disagreeing with the two earlier authors, identified it as an accessory insertion of *M. palmaris longus*.

In this paper we review evidence from development, articulations, topography, and muscle insertions that are relevant to these differing assessments of homology. Also we propose additional research that will permit better discrimination between the two hypotheses. For homology assessments, it is best to compare closely related animals, because their morphologies are similar and the homologies most evident. In this case, the most appropriate comparison is with tree squirrels. Tree squirrels lack the styliiform cartilage, so there is no question about the homology of the pisiform in these animals. There is some disagreement about how tree squirrels and flying squirrels are related to one another, but it is probable that they share a common squirrel (i.e. sciurid) ancestor morphologically similar to *Douglassia jeffersoni* (Emry and Thorington 1982, 1984). Living tree squirrels have changed little from this ancestral morphology and thus provide an excellent comparison for homology assessment in flying squirrels.

Mammalian anatomy is described under several different standards of nomenclature — human anatomy, veterinary anatomy, and comparative anatomy. This problem is particularly acute in the description of wrist anatomy, so we list a series of synonyms for the bones we discuss: Scaphoid bone (=navicular; *os carpi radiale*); Scapholunate bone (=scaphoid + lunate; navicular + lunate; *os carpi radiale* + *os carpi intermedium*); Lunate bone (= *os carpi intermedium*); Triquetrum (=cuneiform; triangular; *os ulnare*); Hamate (=unciform). In addition, Holmgren (1952) uses a series of names for the embryological elements that give rise to the carpal bones — radiale, centrale 1–4, ulnare, radial border cartilage, and ulnar border cartilage — and we follow his terminology.

Discussion

The primitive mammalian arrangement of the carpal bones has recently been reviewed by Lewis (1989) and Stafford and Thorington (1998). The proximal row, from radial to ulnar side, consists of the scaphoid, lunate, and triquetral bones, with the pisiform bone lying palmar to the triquetrum. In most rodents, this is reduced to three bones, presumably by the fusion of the scaphoid and lunate. This is the traditional hypothesis, that the most radial carpal bone in the proximal row (Fig. 1b) is the scapholunate bone. It is based on the extensive comparative study and conclusions of Tullberg (1899), who examined the comparative morphology of the bones, especially their articulations. When both bones are present, the scaphoid and the lunate bones articulate with the radius. The triquetrum and usually the pisiform articulate with the ulna. In most rodents, a single carpal bone articulates with the radius, and it is presumed that the radial side of the lunate has fused with the

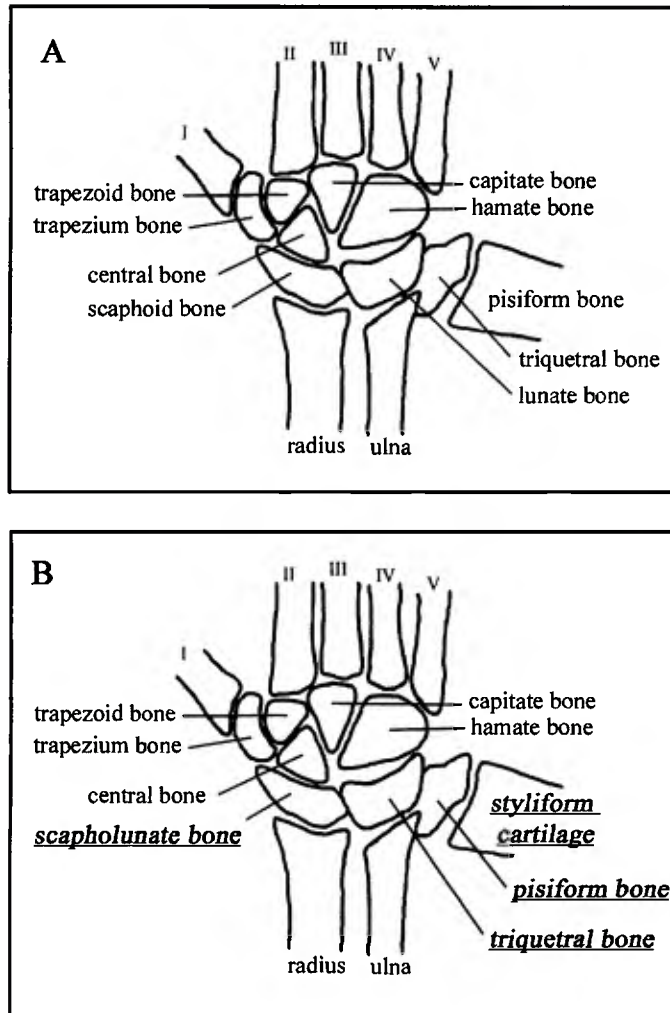


Fig. 1. A) The carpal bones of *Pteromys volans*, labeled according to the carpal homologies hypothesized by Oshida et al. (2000a, b). The styliiform cartilage is hypothesized to be the homologue of the pisiform bone. Illustration modified from Fig. 1c in Oshida et al. (2000a). B) The carpal bones of *Pteromys volans*, labeled according to the traditional carpal homologies. The styliiform cartilage is hypothesized to be the homologue of the hypothenar cartilage. Illustration modified from Fig. 1c in Oshida et al. (2000a).

ulnar side of the scaphoid, forming the scapholunate bone.

The traditional hypothesis is supported by evidence from the fossil record. The only squirrel that lacks the scaphoid-lunate fusion is the Eocene *Douglassia jeffersoni* (Emry and Thorington 1982, 1984). In this fossil, the following wrist bones were recovered: scaphoid, triquetrum, pisiform, and hamate. The authors deduced from four observations that a separate lunate bone had been present but was not recovered. The following comparisons were made with *Sciurus* by Emry and Thorington (1982, 1984), but they are equally valid for *Petaurista*. 1. The scaphoid of *Douglassia* is smaller than the scapholunate of *Sciurus* and appears to be missing the ulnar 1/4 to 1/3 of the bone, relative to the *Sciurus* scapholunate.

2. The proximal articular surface of the scaphoid of *Douglassia* is narrower than the distal articular surface of the radius, whereas the opposite is true in *Sciurus*. 3. The ulnar side of the scaphoid in *Douglassia* has an articular surface that does not articulate with the radial side of the triquetrum. 4. The scaphoid does not articulate with the hamate in *Douglassia*. However, there is a facet on the hamate of *Douglassia* that articulates with the scapholunate in all other squirrels, including *Petaurista*. These observations strongly suggest that there was a separate lunate bone in *Douglassia* and that the most radial carpal bone of the proximal row in all Recent squirrels, including *Petaurista* and other flying squirrels, is the homologue of the fused scaphoid and lunate bones of *Douglassia*. However, direct evidence from a fossil flying squirrel is not available, because most flying squirrels in the fossil record are known only from their teeth.

Embryology also supports the traditional hypothesis that the radial carpal bone of most rodents is the fused scaphoid and lunate bones (Holmgren 1952). The embryological precursors of these bones (the radiale and the centrale 1, in Holmgren's terminology) coalesce very early during chondrification, by the 9.5 mm stage in the laboratory mouse (*Mus musculus*), the 12 mm stage in the Indian striped squirrel (*Funambulus palmarum*), and the 16.5 mm stage in the guinea pig (*Cavia porcellus*). The scaphoid and lunate probably coalesce early in development in all extant squirrels, but no flying squirrels have been studied (Holmgren 1952). Study of carpal development in flying squirrels should clearly delineate between the two hypotheses. The traditional hypothesis predicts that the radiale and the centrale 1 will fuse early in ontogeny. Oshida's hypothesis predicts that they will not fuse and that "radiale" will become the scaphoid and "centrale 1" will become the lunate bone.

Oshida et al. (2000a) clearly identify the most radial carpal bone in the proximal row as the scaphoid and the next as the lunate (Fig. 1a). The reasons for these assessments, although critical to their hypothesis, are not explicitly stated. Their synonyms for the two bones are somewhat confusing — scaphoid (*os carpi intermedioradiale*) and lunate (*os carpi intermedium*). *Os carpi intermedioradiale* is the synonym for the scapholunate, not the scaphoid. *Os carpi intermedium* can not be both a separate lunate and part of the scapholunate at the same time. This confusion may be based on previously published illustrations. There is an illustration of the wrist of *Petaurista*, showing the fusion of *os radiale* and *os intermedium* (Tullberg, 1899: Plate 34, No. 30), which was reproduced (Grassé and Dekeyser, 1955: Fig. 1318) and labeled Ir, os radial et intermediaire soudés [Ir, scaphoid and lunate bones fused]. This was cited by Oshida et al. (2000a, b) and may have led them to list *os carpi intermedioradiale* as a synonym of the scaphoid bone. As noted above, a study of carpal development in flying squirrels would provide the most direct evaluation of the two hypotheses — whether the centrale 1 of Holmgren (1952) is retained as a separate *os carpi intermedium*, the lunate bone, or whether it is fused into an *os carpi intermedioradiale*, the scapholunate bone.

Articular relationships support the traditional hypothesis of carpal bone homology for the bone considered by Oshida et al. (2000a, b) to be the lunate. It has the typical articulations of the triquetral bone. Proximally, it articulates with the ulna. Ventrally, it articulates with the bone traditionally considered to be the pisiform. Distally, it articulates with the hamate bone. Because these are the normal triquetral articulations, and because it is the ulnar-most carpal of the proximal row, it appears to be the triquetrum. If it is, it must be derived embryologically from centrale 4 of Holmgren (1952), as it is in other rodents. If it is

the lunate, as hypothesized by Oshida et al. (2000a, b), then it must be derived from centrale 2 of Holmgren (1952), it must migrate to the ulnar side of the wrist, it must assume a position dorsal to the triquetrum, and it must assume the articulations assumed by centrale 4 in other rodents.

The bone identified as the triquetrum in the Oshida et al. (2000a) hypothesis (Fig. 1a) is considered to be the pisiform bone in the traditional hypothesis (Fig. 1b). Comparative anatomy supports the traditional hypothesis in this assessment. The bone lies palmar to the other bones of the proximal row. It articulates with the ulna and the two other carpal bones of the proximal row, but it does not articulate with the hamate as would be expected of the triquetrum bone. *M. flexor carpi ulnaris* has its major insertion on the distal end of this bone, and *M. abductor digiti minimi* takes origin from it. In these six ways this bone appears to be the pisiform. Oshida et al. (2000a) consider it to be the triquetrum, but they provide no anatomical evidence for this identification.

In all mammals, the pisiform bone is derived embryologically from a palmar element associated with the distal end of the ulna (Holmgren 1952). Therefore embryological study of flying squirrels would clearly discriminate between the two hypotheses. The traditional hypothesis requires that this bone be derived from the palmar element mentioned above. The Oshida hypothesis requires that it be derived from centrale 4, shift into a palmar position, and lose or never form an articulation with the hamate.

The styliiform cartilage is considered not to be homologous with the pisiform bone, in the traditional hypothesis. Instead, Gupta (1966) suggested that it is homologous with an ulnar sesamoid bone that is found in the same place in the wrist of some other mammals. Thorington et al. (1998) and Thorington and Darrow (2000) concluded that the styliiform cartilage is homologous with the hypothenar cartilage of other squirrels, based on several anatomical observations. First, the hypothenar cartilage is absent in flying squirrels but present in all other squirrels. Second, both the hypothenar cartilage and the styliiform cartilage are tightly bound by fascia to the pisiform bone and to the fifth metacarpal. Third, the hypothenar pad is supported by the hypothenar cartilage in most squirrels and by the base of the styliiform cartilage in flying squirrels. Fourth, the hypothenar cartilage is incorporated into the superficial fascia of the hand and the tendon of *M. palmaris longus* in tree and ground squirrels. They identified the muscle inserting on the styliiform cartilage also to be the *M. palmaris longus*.

In contrast, the styliiform cartilage is considered to be derived from the pisiform bone in the hypothesis of Oshida et al. (2000a). These authors provide several reasons for their conclusion. First, they identify the muscle inserting on the styliiform cartilage to be the *M. flexor carpi ulnaris*, which always inserts on the pisiform bone. This interpretation of the anatomy is the same as presented by Gupta (1966) and by Johnson-Murray (1977), who described two tendons of insertion of this muscle, one inserting on the pisiform bone and the other inserting on the base of the styliiform cartilage. Even if this muscle is correctly identified, its insertion can not be used to distinguish between the traditional hypothesis and the Oshida hypothesis. Because it inserts on both the traditional pisiform bone and the styliiform cartilage, either bone could be the homologue of the true pisiform of other mammals. The muscle inserting on the base of the styliiform cartilage is identified as *M. palmaris longus* by Thorington et al. (1997, 1998). If this identification is correct, then it would contradict the Oshida hypothesis and support the hypothesis that the styliiform cartilage is the

homologue of the hypothernar cartilage. Thorington et al. (1997, 1998) describe the muscle taking origin from the medial epicondyle of the humerus superficial to and on the radial side of the *M. flexor carpi ulnaris*. It divides into two heads, one inserting in the palmar fascia and the other inserting on the styliiform cartilage. The muscle fibers and tendon that insert on the styliiform cartilage lie superficial to the *M. flexor carpi ulnaris*. Johnson-Murray (1977) provides a similar less detailed description of the origin of this muscle, but she does not describe its relationship to the *M. palmaris longus*. Gupta (1966) and Oshida et al. (2000a) do not describe the origin. Because *M. palmaris longus* and *M. flexor carpi ulnaris* are both innervated by the ulnar nerve in squirrels (Woods 1972; Thorington et al. 1997), it is not possible to distinguish them by their nerves.

A second reason given by Oshida et al. (2000a) for their homology assessments is the attachment of the flexor retinaculum to the styliiform cartilage. There is complete agreement among authors that palmar ligaments cross the carpal tunnel and connect the falciform bone and the scapholunate to the styliiform cartilage and the traditional pisiform (Gupta 1966; Johnson-Murray 1977; Thorington et al. 1997; Thorington and Darrow 2000; Oshida et al. 2000). The names associated with these ligaments vary among the authors, however. The superficial ligament is called the falciform-styliiform ligament by Johnson-Murray (1977), Thorington et al. (1998), and Thorington and Darrow (2000) (Fig. 2). It is considered part of the flexor retinaculum by Gupta (1966) and Oshida et al. (2000a). Because these ligaments attach to both the traditional pisiform and the styliiform cartilage, their attachments do not

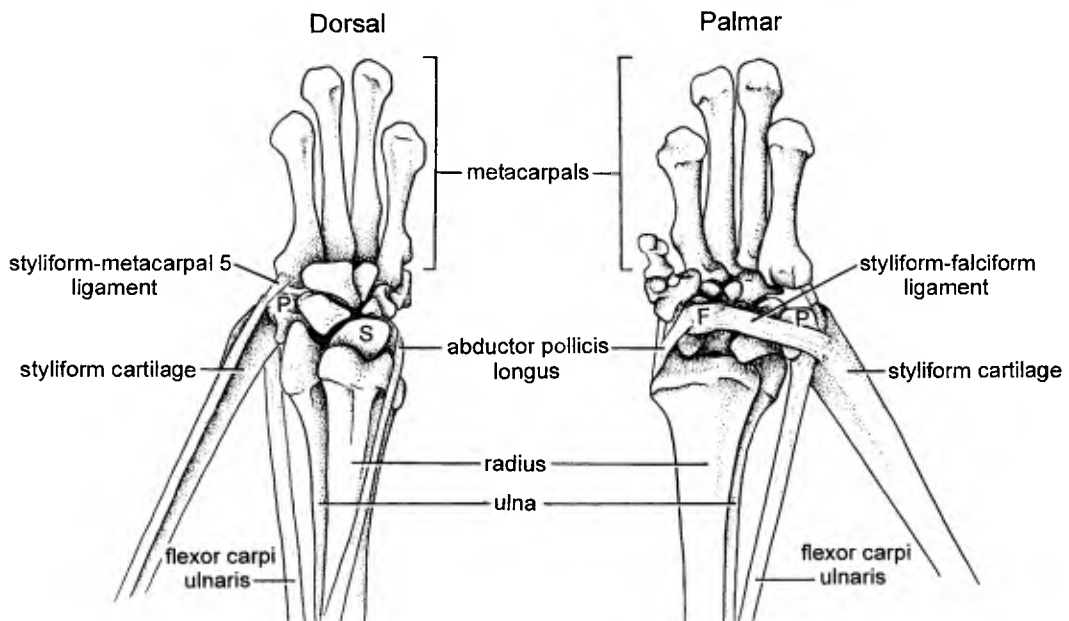


Fig. 2. Dorsal and palmar views of the bones of the left hand of the southern flying squirrel, *Glaucomys volans*, showing tendons and ligaments involved in extending the styliiform cartilage. The transcarpal ligament is not shown; it lies deep to the styliiform-falciform ligament between the pisiform and the scapholunate bones. The *M. flexor carpi ulnaris* is a flexor muscle of the wrist and one of the retractors of the styliiform cartilage (F=falciform bone; P=pisiform bone; S=scapholunate bone). From Thorington et al. (1998).

discriminate between the traditional and the Oshida hypotheses.

The embryological origin of the styliiform cartilage is possibly the ulnar border cartilage, described by Holmgren (1952). This forms on the ulnar side of the wrist in mammals, and in rodents it migrates in a palmar direction and becomes incorporated into the pad of the hand. It is probably the embryological origin of the ulnar sesamoid noted by Gupta (1966) and also of the hypothenar cartilage noted by Thorington et al. (1998) and Thorington and Darrow (2000). If so, the suggested homologies of Gupta and of Thorington et al. can both be correct. Embryological study of flying squirrels would again discriminate clearly between the traditional and the Oshida hypotheses. The traditional hypothesis would be supported if the styliiform cartilage is derived from the ulnar border cartilage. The Oshida hypothesis would be supported by the observations that the styliiform cartilage is derived from the pisiform element and that the ulnar border cartilage degenerates.

An interesting observation made by Oshida et al. (2000b) is the ossification of the styliiform cartilage in old flying squirrels, maintained in captivity. This is listed as additional support for the hypothesis that the styliiform cartilage is derived from the pisiform bone. However, the ossification of the styliiform cartilage does not distinguish between the two hypotheses, because the traditional pisiform always ossifies in rodents. Furthermore, it is not known if ossification occurs in the hypothenar cartilage of other squirrels maintained under similar captive conditions. Therefore, the ossification of the styliiform cartilage does not assist in distinguishing between the traditional and Oshida hypotheses about carpal homologies.

Conclusions

The two hypotheses for the origin of the styliiform cartilage, provided by Thorington et al. (1998) and Oshida et al. (2000a, b) have very different implications for the wrist homologies of flying squirrels. Comparative anatomy favors the traditional hypothesis of carpal homologies, but clearly the best test of the Oshida et al. (2000a, b) hypothesis would be provided by careful embryological study of the wrist of flying squirrels.

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